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edited by Walter E. Boles and Trevor H. Worthy

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Cover image—Australian Museum paleontologist Dr Anne Musser reconstructed the dromornithid *Bullockornis planei* based on fossil remains from the Mid Miocene Camfield Beds, Northern Territory, Australia, and on morphology known to be typical of large flightless birds. Understanding morphology in living and extinct life forms, and discovering the relationship between structure, function and phylogeny, is an essential part of research at the Australian Museum. It leads us to better understand how life adapts, or sometimes fails to adapt, to a changing world.

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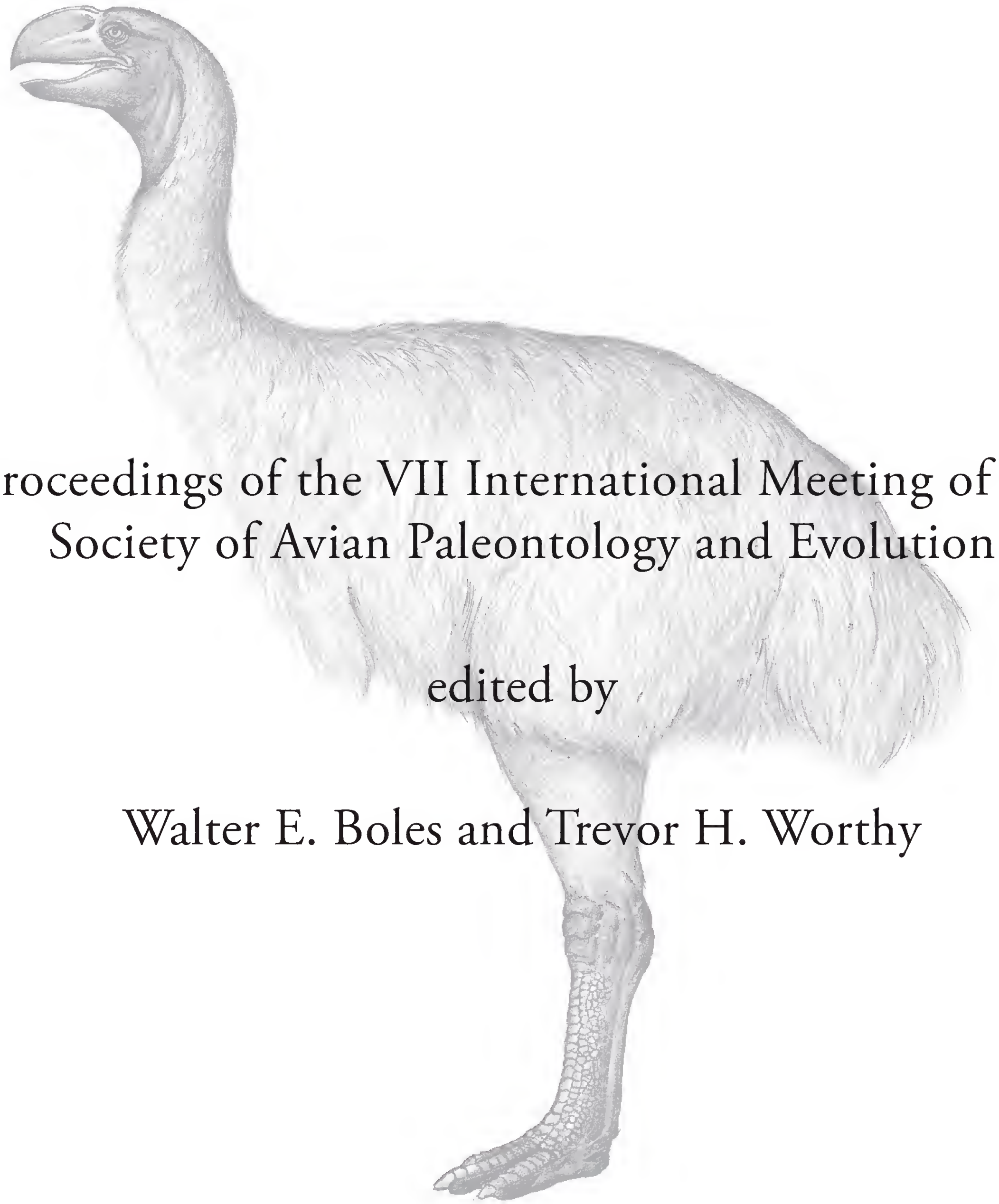

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Walter E. Boles and Trevor H. Worthy

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Foreword

This volume comprises the Proceedings of the VII International Meeting of the Society for Avian Paleontology and Evolution (SAPE). The previous six meetings were held in North America, Europe and China. This seventh meeting marks the first gathering of the Society in the Southern Hemisphere. It was hosted by, and held at, the Australian Museum, in Sydney, from 18–23 August, 2008.

The comparative remoteness of Australia, coupled with a global economic downturn at that time, limited the number of members to fewer than had attended previous meetings. Nonetheless, it was an excellent meeting, the 40 participants representing 11 countries enjoying here the company of a good turnout of Australian and New Zealand paleontologists. Consequently, the results of a large number of Australian- and New Zealand-based studies were presented, more than at previous meetings.

The sixteen works in this volume reflect the full range of the 40 talks and posters presented at the Meeting. The topics were wide-ranging, addressing, among other things, progress in some of the world's most developed faunas, such as Messel and Green River, the amazing insights into early avian evolution emerging from the Chinese deposits, and the recently uncovered and highly intriguing St Bathan's locality in New Zealand. The diverse research directions of SAPE members, while united by a common interest in avian evolution, was very evident. For example, the period of interest include Mesozoic (8 presentations), Tertiary (15), Quaternary (9), and Modern, including DNA, (8). By subject area, the categories included taxonomy/phylogeny (20), anatomy (11), ecology (2) and biogeography/phylogeography (7). Some members dealt with only a single taxon, while others looked at birds on a global scale. The developing role of DNA in unravelling avian phylogenies and its synergy with fossil analyses was addressed in four papers, and a group discussion, led by Per Ericson, focussed on the integration of molecular data with the fossil record. A novel component of the scientific program at this meeting was a President's Lecture, given by Ken Campbell on The Automated Balance System in Birds.

Presenters at the meeting encompassed a wide range of experience. The paleontologists of long standing were able to enjoy the enthusiasm and interest of a number of students and early career workers—the next generation of avian paleontology.

At previous meetings, there has been one or more field trips to local fossil sites that have bird remains. No such location exists close to Sydney, so the opportunity was taken to visit sites at which representatives of the characteristic and restricted extant Australian bird families could be encountered. Trips were run on two days, visiting rainforests, wetlands and woodland, with most target groups successfully observed.

At the business meeting, Per Ericson was elected as President and Trevor Worthy as Vice-President, while Gerald Mayr and David Steadman remain as Secretary and Treasurer, respectively. The new Executive Council consists of five Members-at-large: Estelle Bourdon, Anusuya Chinsamy-Turan, Ursula Göhlich, Jorge Noriega and Marcel van Tuinen. Members voted to accept the invitation from the Naturhistorisches Museum Wien, Austria, to host the next meeting in 2012.

Many thanks go to Jaynia Sladek (Bird Section, Australian Museum), who was indispensible and responsible for so much of the organization; Dr Les Christidis, who in his role as Assistant Director, Research and Collections, encouraged the Museum to offer to host this meeting at the previous gathering in Quillan, France; Dr Anne Musser (Australian Museum) for the artwork that adorned the scientific program cover (and this cover) and conference t-shirts; the Australian Museum, for making the facilities and staff available for hosting the meeting, and particularly Venues (Mark Connolly and Scott Gilkeson), for ensuring that the rooms and catering worked smoothly; Dr Shane McEvey, The Editor, Records of the Australian Museum, for producing this volume with minimal problems or delays; to all the authors and referees who contributed to this volume; and to all the participants at the meeting, whether presenting or not, for guaranteeing an informative and enjoyable meeting.

WALTER E. BOLES AND TREVOR H. WORTHY

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Delegates to the VII International Meeting of the Society of Avian Paleontology and Evolution, Sydney, 18–23 August 2008. Front row (left to right): Gary Kaiser (USA), Jenny Worthy (Australia), Trevor Worthy (Australia), Ken Campbell (USA), Per Ericson (Sweden), Tommy Tyrberg (Sweden), Gerald Mayr (Germany). Second row (left to right): Luis Chiappe (USA), Teresa Tomek (Poland), Zbigniew Bocheński (Poland), Ursula Göhlich (Austria), Albrecht Manegold (Germany), Ilka Weidig (Germany), Zhiheng Li (China), Hanneke Meijer (Netherlands), Kari Prassack (USA). Third row (left to right): Alyssa Bell (USA), Priscilla Gaff (Australia), Estelle Bourdon (France), Paul Scofield (New Zealand), Alan Tennyson (New Zealand), Jackie Nguyen (Australia), Zhonghe Zhou (China), Brian Gill (New Zealand), Janette Norman (Australia). Fourth row (left to right): Andrzej Elzanowski (Poland), Gillian Gibbs (New Zealand), Roger Close (Australia), Robert Jones (Australia), Anne Musser (Australia), Nic Rawlence (Australia), Kate McCarville (USA), Anita Gamauf (Austria), Alan Lamm (Australia). Fifth row (left to right): Gareth Dyke (Ireland), Jingmai O'Connor (USA), Walter Boles (Australia). Present but not pictured: Sylvia Hope (USA), Mike Dickison (New Zealand), Matt Phillips (Australia), Les Christidis (Australia), Jaynia Sladek (Australia).

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A Reassessment of *Sinornis santensis* and *Cathayornis yandica* (Aves: Enantiornithes)

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ABSTRACT. The taxonomy of the first two enantiornithine birds named from the Early Cretaceous of China, *Cathayornis yandica* and *Sinornis santensis*, has remained controversial despite the relative completeness of both holotype specimens. This is because *C. yandica* is regarded as a junior synonym of *S. santensis* by some researchers, and as a distinct taxon by others. This question is revisited in this paper; in order to determine the validity of *C. yandica*, we conduct a detailed morphological review of both holotype specimens. Despite proposed synonymy we argue that there are clear and distinct anatomical differences between the two taxa; indeed our morphological observations demonstrate that the two birds constitute valid and distinct branches in the diverse enantiornithine evolutionary radiation. Of course, and like many other groups of fossil vertebrates, the diverse Cretaceous bird lineage Enantiornithes requires taxonomic revision yet in the case of *C. yandica* and *S. santensis* we attribute much of the confusion to: (1) incomplete specimens being designated as holotypes, and (2) the absence of clear morphological character-based taxon diagnoses founded on rigorous anatomical comparisons.

O'CONNOR, JINGMAI, & GARETH DYKE, 2010. A reassessment of *Sinornis santensis* and *Cathayornis yandica* (Aves: Enantiornithes). In *Proceedings of the VII International Meeting of the Society of Avian Paleontology and Evolution*, ed. W.E. Boles and T.H. Worthy. *Records of the Australian Museum* 62(1): 7–20.

Enantiornithes are the most diverse known lineage of Mesozoic birds (Chiappe, 2002; Chiappe & Dyke, 2007; Dyke & Nudds, 2009) with over 60 species named, and in China dozens, if not hundreds, of undescribed specimens (O'Connor, 2009). However, despite this apparent diversity, the taxonomy of Enantiornithes remains largely unreviewed and at least a third of named species are based upon extremely fragmentary, sometimes non-overlapping, fossil material (Table 1) (for example, six named species from the Cretaceous of Uzbekistan are based on coracoid fragments; Panteleyev, 1998) (see O'Connor, 2009). While revisions have been limited, several taxa have nevertheless been questioned and re-evaluated: *Nanantius valifanovi* has been synonymized under *Gobipteryx minuta* (Chiappe *et al.*, 2001); *Cathayornis yandica* under *Sinornis santensis* (Sereno *et al.*, 2002); *Liaoxiornis delicatus* and *Lingyuanornis parvus* have been considered Euenantiornithes indeterminant (Chiappe *et al.*, 2007); and *Aberratiodontus gui* has been synonymized under *Yanornis martini* (Zhou *et al.*, 2008a). Of these revisions to the taxonomy of Enantiornithes, most have passed largely unquestioned into subsequent literature with the exception of the proposed synonymy of *Cathayornis yandica* and *Sinornis santensis*, in which there is no consensus (cf. Li *et al.*, 2006; Chiappe *et al.*, 2007; Cau

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& Arduini, 2008). In this paper we provide a review of this issue and a detailed morphological study which supports the validity of *C. yandica* as a separate taxon from *S. santensis.*

Unnamed or unpublished material is referred to by collection number with the institutional prefix. Relevant institutional acronyms are BNHM (Beijing Natural History Museum, Beijing), IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing), DNHM (Dalian Natural History Museum, Dalian), CAGS (Chinese Academy of Geological Sciences, Beijing), GMV (Geological Museum of China, Beijing), LP (Institut d'Estudis Illerdencs, Lleida, Spain).

Background

In recent years the extremely rapid rate of new discoveries of fossil birds from China has resulted in publications presenting strikingly similar taxa sometimes appearing almost simultaneously (e.g., Zhou *et al.*, 1992; Sereno & Rao, 1992; see also Hou & Chen, 1999; Ji & Ji, 1999; Zhou & Zhang, 2001; Gong *et al.*, 2004), as was the case with the descriptions of *Sinornis santensis* (Beijing Natural History Museum, Beijing; BNHM BPV 538a,b) [Sereno & Rao, 1992] and *Cathayornis yandica* (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; IVPP V9769a,b) [Zhou *et al.*, 1992], the first two enantiornithine birds described from China (Sereno & Rao, 1992, Sereno *et al.*, 2002, Zhou *et al.*, 1992). Owing to the rapid rate of discovery and publication, detailed comparisons of Chinese fossil birds have often been absent and thus diagnostic distinctions between 'species' have often been left unclear or are later proven to be unverifiable from the original publications (i.e., through photographs and figures) (e.g., Hou, 1997; Zhang *et al.*, 2006; Li *et al.*, 2006; Gong *et al.*, 2008). This was certainly the case in the original publications of *S. santensis* (Sereno & Rao, 1992) and *C. yandica* (Zhou *et al.*, 1992).

In a publication a decade after it was first named, *C. yandica* was synonymized under *S. santensis* by Sereno *et al.* (2002), while in the same volume an argument was made for the validity of the former (*C. yandica*; Zhou & Hou, 2002). Synonymy was not strongly supported (or refuted) empirically in either chapter and as a result *C. yandica* and *S. santensis* are still treated as distinct taxa by some (Li *et al.*, 2006; Chiappe *et al.*, 2006) and as synonyms by others (Chiappe *et al.*, 2007; Cau & Arduini, 2008).

The situation has been further complicated by the subsequent referral of additional species to the genus *Cathayornis*: *C. caudatus* [Hou, 1997], *C. aberransis* [Hou *et al.*, 2002], and *C. chabuensis* [Li *et al.*, 2008]. Given that the validity of *C. yandica* is uncertain, the assignment of new specimens and/or species to *Cathayornis* first needs to be justified with morphological support for the validity of the original genus (as independent from *Sinornis*). This then needs to be followed by morphological support for a close relationship between the new specimen and the holotype of *C. yandica*, as well as identifying distinguishing features that indicate the specimen is a new species. The issue of the proposed synonymy with *Sinornis* has not been discussed, and thus these species require re-evaluation.

In Enantiornithes, diagnosing a new species or justifying higher-level relationships can be particularly difficult. Enantiornithine birds are usually small and morphologically uniform—like their extant perching passerine counterparts. Without very detailed inspection, small morphological differences may go unobserved and multiple 'real' species may be regarded under one taxon (e.g., Martin & Zhou, 1997; Zhou, 2002). Alternatively, without good preservation and preparation of these small specimens, it is difficult to separate true morphologies from those that may be diagenetic or taphonomic (e.g., flattening, crushing, bending). Currently, despite the known diversity of enantiornithines (Table 1), the inter-relationships of taxa and evolutionary trajectories within the clade remain poorly understood (but see O'Connor, 2009). Resolution is required within enantiornithine taxonomy so that studies of enantiornithine biology, phylogenetics and lineage dynamics can proceed (Chiappe & Walker, 2002; Chiappe *et al.*, 2007; Dyke & Nudds, 2009; O'Connor, 2009).

The holotype specimens of *S. santensis* and *C. yandica* are both small fossil birds, comparable to one another in size and with a similar mode of preservation in which the bones are preserved as voids in a slab and counterslab (Figs 1, 2). Because their bones are not preserved, moulds and casts have been made from the specimens to facilitate their study; these casts are much more informative than the original slabs. Both the slab and counterslab of the *C. yandica* holotype were studied from the original and the cast (IVPP V9769a,b), the main slab of *S. santensis* was studied from a cast (BNHM BPV 538a,b), and both slabs were studied from original photographs. Both holotype specimens were collected in the northwest of Liaoning Province, northeastern China near Chaoyang City. The holotype of *C. yandica* was collected from the Xidagou locality, just south of Boluochi, while *S. santensis* was discovered just west of Shengli (Hou, 1997; Zhou & Hou, 2002).

However, although the specimens are similar in preservation, the discernable information that can be gained from each differs greatly (Figs 1,2). While the holotype of *C. yandica* (IVPP V9769a,b) is largely disarticulated and incomplete (Fig. 1), that of *S. santensis* is preserved in articulation but is also missing some elements (BNHM BPV 538a,b) (Fig. 2). The two specimens almost exactly mirror each other in terms of well-preserved skeletal elements: the holotype of *C. yandica* (IVPP V9769a,b) includes a fairly well-preserved skull and pectoral girdle but its pelvic girdle and hindlimbs are incomplete and disarticulated, while the holotype of *S. santensis* (BNHM BPV 538a,b) preserves an articulated pelvic girdle and hindlimbs but has a poorly preserved partial skull and pectoral girdle. Thus, characters used to distinguish *S. santensis* (note that a diagnosis is absent from the original publication; Sereno & Rao, 1992) are difficult to assess in *C. yandica* (e.g., the presence of a blade-like ischium in *C. yandica*; Sereno & Rao, 1992) and vice versa (e.g., the presence of notches in the sternum of *S. santensis*; Zhou *et al.*, 1992).

The original publications on *S. santensis* and *C. yandica* did not directly compare the two specimens (Sereno *et al.*, 2002). The first paper (Sereno & Rao, 1992) on *S. santensis* also lacked a formal diagnosis and thus there were no clear morphologies to compare with other known taxa at the time (Sereno & Rao, 1992). Later a proper diagnosis was provided for the taxon (Sereno *et al.*, 2002) but all the morphologies cited have since been recognized as general synapomorphies of enantiornithines or more exclusive clades within such as Euenantiornithes (Chiappe & Walker, 2002; O'Connor, 2009), with the possible exception of the 'scimitar-shaped' ischium (Sereno *et al.*, 2002). In contrast, the original publication on *C. yandica* (Zhou *et al.*, 1992) provided a very thorough diagnosis, however most of the characters cited in this description, although rare features at the time, are now known to have a wide distribution throughout Aves (e.g.,

Table 1. Published records of enantiornithine birds listed chronologically. Abbreviations: AUS, Australia; EUR, Europe; N-AM, North America; S-AM, South America.

binomial	co	year	material	binomial	co	year	material
Gobipteryx minuta	Asia	1974	partial skull and mandible	Enantiornithes indet.	AUS	1999	proximal tibiotarsus
Alexornis antecedens	N-AM	1976	leg/wing bones	Enantiornithes indet.	AUS	1999	distal tibiotarsus
Gobipteryx minuta	Asia	1976	partial skull and mandible	Enantiornithes indet.	AUS	1999	distal tibiotarsus
Enantiornis leali	S-AM	1981	isolated coracoid, scapula and humerus	*Eoenantiornis buhleri*	Asia	1999	complete w/ feathers in single slab
Gobipteryx minuta	EUR	1981	two partial skeletons, bone fragments	*Gurilynia nessovi*	Asia	1999	humerus fragments and a partial coracoid
Kizylkumavis cretacea	Asia	1984	partial humerus	*Hebeiornis fengningensis*	Asia	1999	nearly complete specimen in slab
Zhyraornis kashkarovi	Asia	1984	partial synsacrum	*Liaoxiornis delicatus*	Asia	1999	complete in slab
Zhyraornis logunovi	Asia	1984	partial synsacrum	*Lingyuanornis parvus*	Asia	1999	complete in counterslab
Avisaurus archibaldi	N-AM	1985	tarsometatarsus	*Cathayornis aberransis*	Asia	2000	partial skeleton in slab
Nanantius eos	AUS	1986	tibiotarsus	*Protopteryx fengningensis*	Asia	2000	two nearly complete specimens
Noguerornis gonzalezi	EUR	1989	partial skeleton	Euenantiornithes indet.	EUR	2001	pellet
Sazavis prisca	Asia	1989	partial tibiotarsus	*Gobipteryx minuta*	Asia	2001	partial skull
Cathyaornis yandica	Asia	1992	nearly complete in slab and counterslab	*Longipteryx chaoyangensis*	Asia	2001	two nearly complete specimens
Concornis lacustris	EUR	1992	postcranial skeleton in single slab	*Avisaurus archibaldi*	N-AM	2002	distal metatarsal III
Neuquenornis volans	S-AM	1992	partial skeleton	Enantiornithes indet.	EUR	2002	tibiotarsus
Sinornis santensis	Asia	1992	nearly complete in slab	Enantiornithes indet.	Asia	2002	right humerus, incomplete
Enantiornis martini	Asia	1993	partial coracoid	Enantiornithes indet.	S-AM	2002	partial right half of a mandible
Enantiornis walkeri	Asia	1993	partial coracoid	*Eocathayornis walkeri*	Asia	2002	proximal skeleton in slab and counterslab
Lectavis bretincola	S-AM	1993	isolated tibiotarsus and tarsometatarsus	*Halimornis thompsoni*	N-AM	2002	scapula, humerus, femur and pygostyle
Otogornis genghisi	Asia	1993	wing in slab	*Iberomesornis romerali*	EUR	2002	two partial skeletons
Soroavisaurus australis	S-AM	1993	two tarsometatarsi	*Longirostravis hani*	EUR	2003	nearly complete in single slab
Yungavolucris brevipedalis	S-AM	1993	five isolated tarsometatarsi	*Aberratiodontus wui*	Asia	2004	nearly complete in slab and counterslab
Avisaurus gloriae	N-AM	1995	tarsometatarsus	*Vescornis hebeiensis*	Asia	2004	nearly complete in single slab
Boluochia zhengi	Asia	1995	partial skeleton in slab	Enantiornithes indet.	Asia	2005	isolated wing in single slab
Eoalulavis hoyasi	EUR	1996	partial skeleton in single slab	*Dalingheornis liwei*	Asia	2006	nearly complete in slab
Euenantiornithes indet.	Africa	1996	isolated bone fragments	*Dapingfangornis sentisorhinus*	Asia	2006	nearly complete in single slab
Lenesornis maltshevskyi	Asia	1996	partial synsacrum	*Elsornis keni*	Asia	2006	partial skeleton
Nanantius valifanovi	Asia	1996	partial skeleton	Enantiornithes indet.	Asia	2006	isolated wing in single slab
Avisaurus n.sp.	N-AM	1997	partial skeleton	Enantiornithes indet.	Asia	2006	partial pelvis and hindlimbs
Cathayornis caudatus	Asia	1997	partial skeleton in slab	Euenantiornithes indet.	Asia	2007	nearly complete in slab
Cuspirostrisornis houi	Asia	1997	proximal skeleton in single slab	Euenantiornithes indet.	Asia	2007	nearly complete in slab
Euenantiornithes indet.	EUR	1997	proximal skeleton in slab	*Martinavis cruzyensis*	EUR	2007	humerus
Largirostrornis sexdentornis	Asia	1997	nearly complete in slab	*Martinavis* sp.	S-AM	2007	four humeral fragments
Longchengornis sanyanensis	Asia	1997	partial skeleton in slab	*Martinavis vincei*	S-AM	2007	complete humerus
Longirostrisornis	Asia	1997	partial skeleton in slab	*Martinavis vincei*	S-AM	2007	distal humerus
Abavornis bonaparti	Asia	1998	partial coracoid	*Paraprotopteryx gracilis*	Asia	2007	nearly complete slab and counterslab
Abavornis sp.	Asia	1998	partial coracoid	*Alethoalaornis agitornis*	Asia	2008	five nearly complete slab specimens
Alexornithiformes indet.	Asia	1998	partial coracoid	*Cathayornis chabuensis*	Asia	2008	partial skeleton in slab and counterslab
Catenoleimus anachoretus	Asia	1998	partial coracoid	*Enantiophoenix electrophyla*	EUR	2008	partial skeleton w/ feathers
Enantiornithes indet.	EUR	1998	partial femur and coracoid	Enantiornithes indet.	EUR	2008	femur
Explorornis nessovi	Asia	1998	partial coracoid	Enantiornithes indet.	EUR	2008	tarsometatarsus
Explorornis sp.	Asia	1998	partial coracoid	*Pengornis houi*	Asia	2008	nearly complete in single slab
Explorornis sp.	Asia	1998	partial coracoid	*Rapaxavis pani*	Asia	2009	complete in single slab
Incolornis martini	Asia	1998	partial coracoid	*Shanweiniao cooperorum*	Asia	2009	nearly complete in slab and counterslab
Incolornis silvae	Asia	1998	partial coracoid	DNHM D2950/1	Asia	2010	nearly complete in slab and counterslab

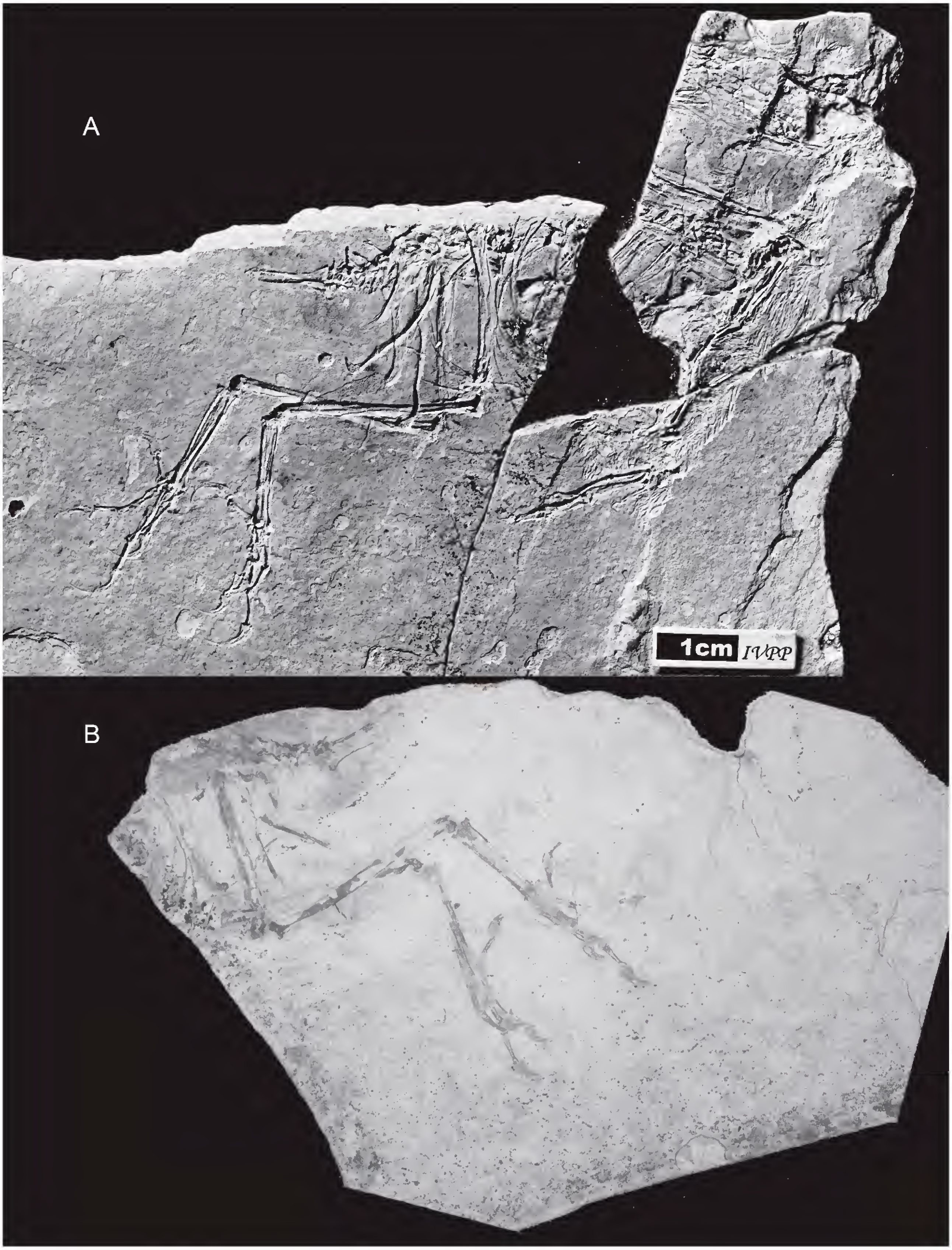

Figure 1. Photograph of the slab and counterslab of *Sinornis santensis*: (*A*), BNHM BPV 538a; and (*B*), BNHM BPV 538b. Scale bar equals 10 mm. Photographs from Zhou Zhonghe (*A*) and Luis Chiappe (*B*).

strut-like coracoid, low keel on sternum, straight scapula, toothed premaxilla and dentary, clawed manus; Zhou *et al*., 1992; O'Connor, 2009; O'Connor *et al*., 2009). Following the subsequent deluge of Chinese fossil discoveries, an updated diagnosis that distinguishes the specimen from other taxa was provided (Zhou & Hou, 2002).

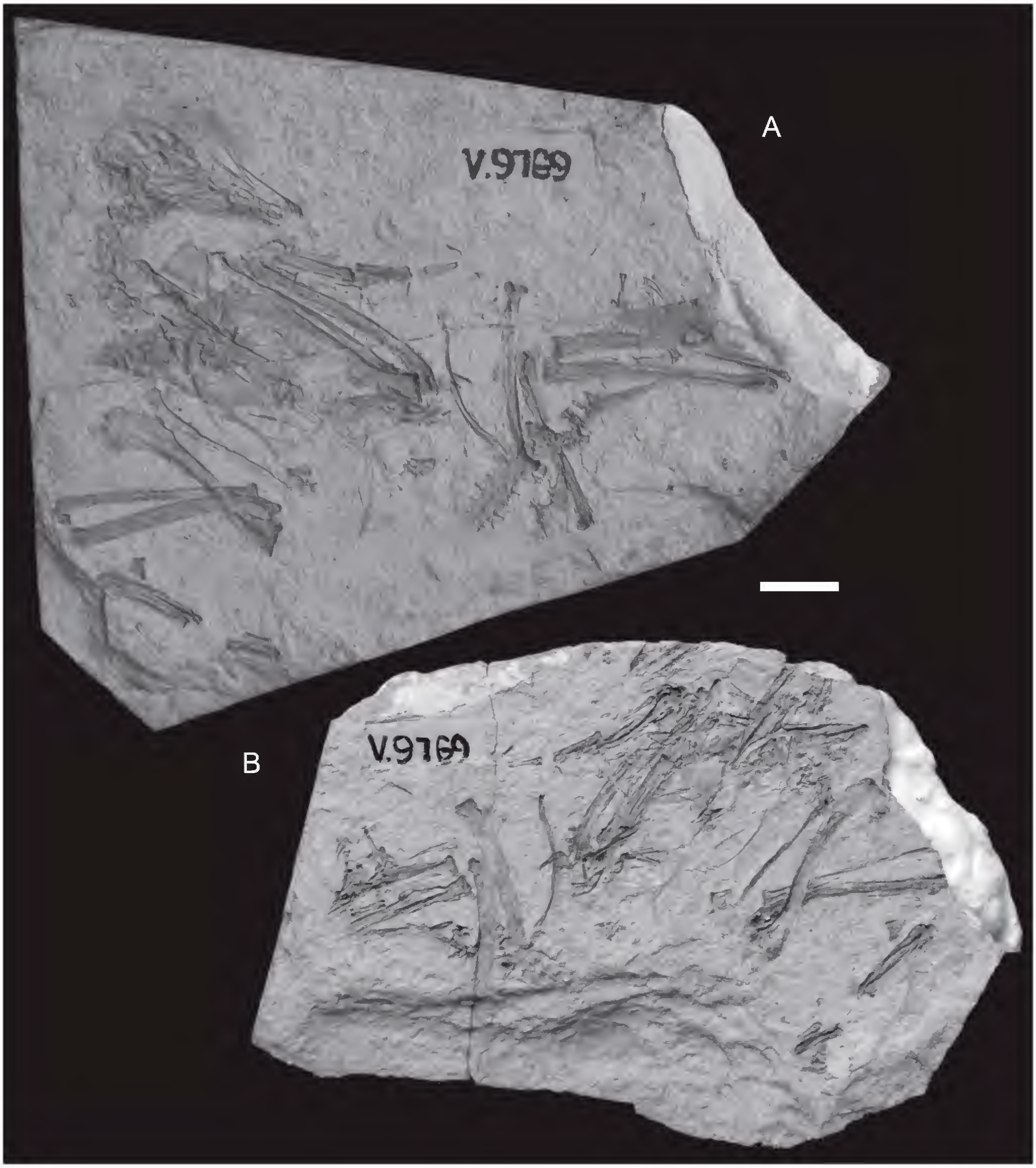

Figure 2. Photograph of *Cathayornis yandica*: (*A*) IVPP V9769a; and (*B*) IVPP V9769b. Scale bar equals 10 mm.

Arguments for the synonymy of the two taxa are based on morphology (Sereno *et al*., 2002). Despite having identified differences between the two holotype specimens, including differences in size, proportions of the manual claws, and the morphology of the minor digit, Sereno *et al*. (2002) nevertheless used similarities in preserved pygostyle and ischium morphology as primary arguments for the synonymy of the two species. Zhou & Hou (2002) also discussed the issue of synonymy and provided clear diagnoses for both species which included morphological differences, some of which were also recognized by Sereno *et al*. (2002). Zhou & Hou (2002) also argued that the locality difference alone may be enough to justify separating the two taxa.

Cathayornis yandica vs. *Sinornis santensis*

Locality. The holotype specimens of *S. santensis* and *C. yandica* were described from different localities in the Early Cretaceous Jiufotang Formation (upper Jehol Group: 120 Ma; Zhou, 2006), approximately 10 km apart, with Chaoyang City as the closest major geographic indicator (Sereno *et al*., 2002; Zhou & Hou, 2002; Zhou & Zhang, 2006). Although this has been used to distinguish the two taxa, differentiation based on inferred geological age, or geographical separation, makes assumptions about a species range or success. Among extant birds there are many examples of species that have huge geographical ranges, thus such assumptions are for obvious reasons inherently weak. The error associated with dating sediments is typically large and limiting an extinct taxon based on knowledge of an extant analogue bears no validity other than a proposed possibility. Comparisons with geographical ranges of similar (e.g., diet, ecology, size, etc) modern taxa or average species duration through time may be used as valid arguments for erecting a new taxon, however, such arguments should be made only when they can be justified and well supported by cited data. In the case of *S. santensis* and *C. yandica*, no detailed justification has been provided.

Morphology. All the morphological variation that has been previously used to either support the existence of two species, or the synonymization of *C. yandica* under *S. santensis*, is reviewed here. Some previously published data are questioned and alternative interpretations of the preserved features are provided. Note that, although a size difference of approximately 10% is present between the two holotype specimens (Sereno *et al*., 2002; Zhou & Hou, 2002), because the ontogenetic stage of each specimen is unknown (this aspect of enantiornithine biology also remains unclear) this difference should not be considered diagnostic until further explored through histological analysis. Furthermore, this size differential falls well within the typical size range for a comparably-sized species of living bird (Dunning, 1993).

Skull. Despite the very poor preservation of the skull in the *S. santensis* holotype, from which little or no information can actually be gained (Figs 1, 3B), Sereno *et al*. (2002) compared the morphology of the nasals and maxilla of the two specimens (Fig. 3). Both were described as possessing broad nasals which expand caudal to the external nares and have a triangular caudal margin (Sereno *et al*., 2002). We concur that the nasal of the holotype of *C. yandica* is well-preserved; the nasals articulate medially for approximately half their length, separated rostrally by the nasal (frontal) processes of the premaxilla and caudally by the frontals (Fig. 3A). The rostrally directed maxillary and premaxillary processes are sharply tapered; of these, the maxillary process is fairly short, although contributing to the lateral border of the external nares (in contrast with taxa in which this process is absent and the nasal contribution to the external nares is restricted to the caudal and dorsal margins, e.g., DNHM D2950/1, *Rapaxavis pani* and *Longipteryx chaoyangensis*; Zhang *et al*., 2000; Morschhauser *et al*., 2009; Wang *et al*., 2010). In *S. santensis*, however, no nasal can be definitively identified because the skull is comprised of numerous incomplete bone fragments, none of which preserve any morphology that allows unequivocal identification. Even if Sereno & Rao (1992) are correct and some bone fragments that are in articulation with what has been interpreted as the frontal (Sereno & Rao, 1992) are indeed nasals (Fig. 3B), with only the caudal half of this region preserved we cannot determine if they were expanded (relative to the rostral half).

The caudal half of the maxilla of *S. santensis* was described as differing from that of *Archaeopteryx* because its dorsal and ventral margins are parallel and the jugal ramus does not taper significantly caudally (Sereno *et al*., 2002). These details are impossible to verify, however, because neither holotype specimen, *S. santensis* or *C. yandica*, has a maxilla that clearly preserves this region (Fig. 3). The left maxilla in the *C. yandica* holotype is visible nearly in articulation with the premaxilla; the premaxillary and jugal rami appear subequal (as opposed to the elongate premaxillary ramus in longipterygids; O'Connor *et al*., 2009). The maxilla of *C. yandica* has a long and thin caudodorsally directed nasal process; the caudal articulation with the jugal is not completely preserved so we cannot rule out that the jugal ramus was tapered, although, in its preserved portions, this ramus does have parallel rostral and dorsal margins. In *S. santensis*, the maxilla is even less clear; one element may represent the maxilla based on the presence of what appears to be a nasal process, as in *C. yandica* (absent in *Gobipteryx minuta*; Chiappe *et al*., 2001) (Fig. 3B). If correct, the premaxillary ramus is not preserved; the dorsal and ventral margins of the jugal ramus are parallel except for the distalmost articulation with the jugal where this process tapers abruptly (as opposed to the slow tapering of this process in *Archaeopteryx*; Elzanowski, 2002), morphologically similar to *Hebeiornis fengningensis* (= *Vescornis hebeiensis*; Xu *et al*., 1999; Zhang *et al*., 2004). We conclude that, given the skull preservation in the holotype of *S. santensis*, no cranial morphologies are useful for either distinguishing, or aligning, the two taxa.

Vertebral column. While on the one hand we agree with Sereno *et al*. (2002) that the thoracic vertebral morphology preserved in the holotypes of *S. santensis* and *C. yandica* are comparable, this region of the skeleton is generally conserved among Early Cretaceous enantiornithines (Chiappe & Walker, 2002) and neither specimen preserves any deviant morphologies (O'Connor, 2009). Note however that while Sereno *et al*. (2002) recorded the number of sacral vertebrae as eight in *S. santensis*, it is impossible to count in this region of the skeleton because the articulated pelvic girdle is preserved in lateral view, obscuring the sacrals from view (Fig. 1).

The pygostyles of *S. santensis* and *C. yandica*, as noted by Sereno *et al*. (2002), are also morphologically very similar, with dorsal and ventral processes that reach beyond the articular facet and ventrolaterally directed processes that rapidly diminish distally, causing a marked taper (Sereno *et al*., 2002; Zhou & Hou, 2002) (Fig. 4). Since the discovery of these specimens, however, several new species have been described that possess the same morphology, now regarded as typical of most enantiornithines (Zhang *et al*., 2000; Chiappe & Walker, 2002; Chiappe *et al*., 2002; Li *et al*., 2006; O'Connor, 2009). As noted by Zhou & Hou (2002), the pygostyles of the two taxa do differ in length with respect to their overall body size, which can only be considered a true morphological difference and thus a diagnostic character: the pygostyle of *C. yandica* is nearly 25% longer than that of *S. santensis* (Fig. 4).

Thoracic limb. Zhou & Hou (2002) listed differences in the morphology of the ulnare as a diagnostic distinction between the two taxa: the ulnare of *C. yandica* is described as having a larger metacarpal incision than that of *S. santensis* (Zhou & Hou, 2002). The ulnares certainly differ in morphology between the two specimens (Fig. 5); the ulnare in the holotype specimen of *S. santensis* (Fig. 5B) is much more U-shaped, with a deeper and narrower incision relative to that of *C. yandica*, which is much shallower and wide (*sensu* Zhou & Hou, 2002). The fairly deep incisure preserved in the *S. santensis* holotype was noted by Sereno & Rao (1992) and compared to the ulnare morphology of more derived birds such as *Ichthyornis*. The narrow and deep metacarpal incisure on the ulnare of *S. santensis* differentiates this taxon from *C. yandica*.

The morphology of the manus is also similar in both species (Fig. 5): *S. santensis* and *C. yandica* have small claws

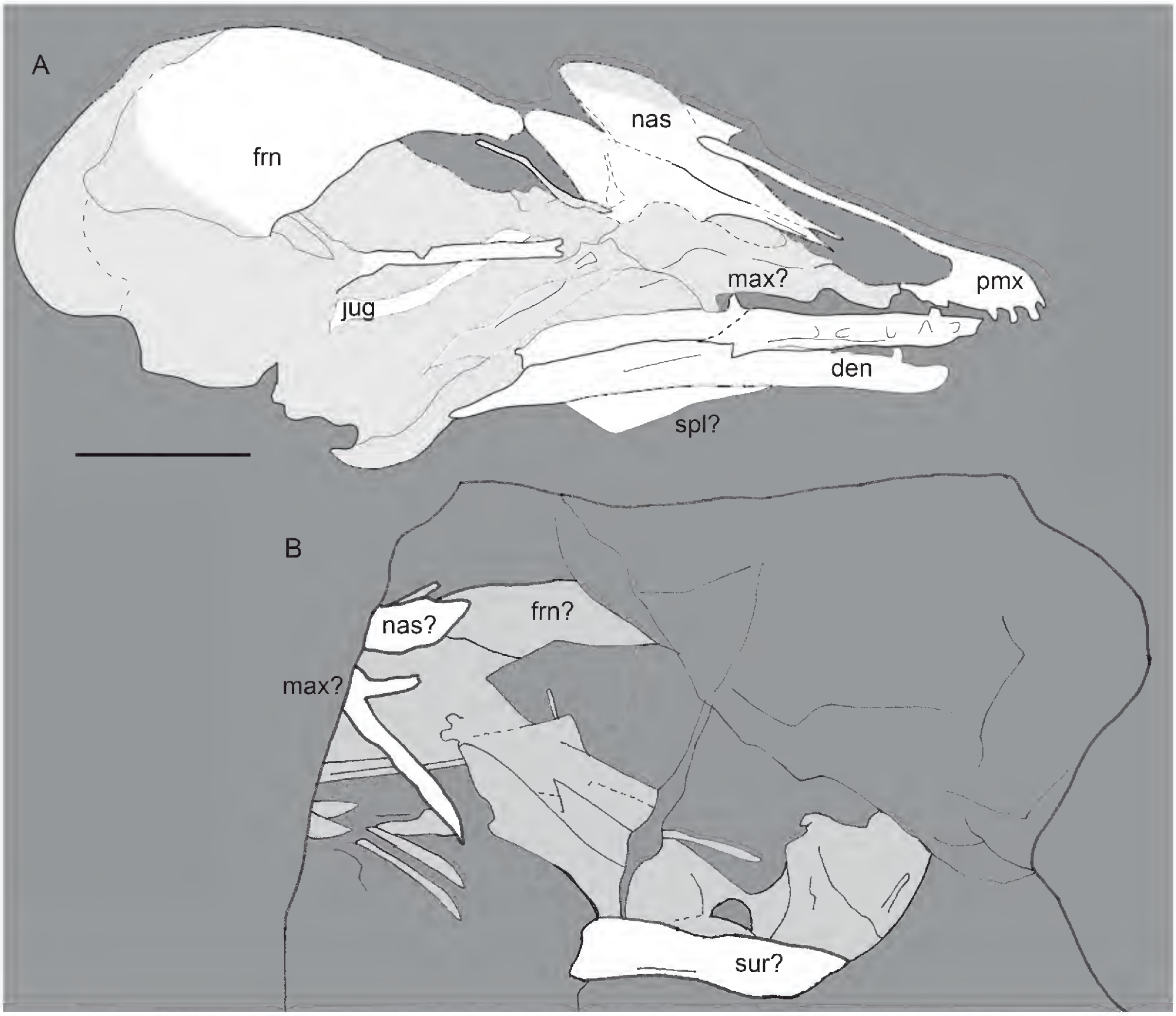

Figure 3. Camera lucida drawings of the skull of: (*A*) *Cathayornis yandica* (from cast of IVPP V9769a); (*B*) *Sinornis santensis* (from cast of BNHM BPV 538a). Abbreviations: *den*, dentary; *frn*, frontal; *jug*, jugal; *max*, maxilla; *pmx*, premaxilla; *spl*, splenial; *sur*, surangular. Question marks denote equivocal determinations.

on both their alular and major digits and have short alular digits that do not distally surpass the distal end of the major metacarpal. The proximal carpometacarpus was considered to be unfused in *S. santensis* as opposed to fused in *C. yandica* (Sereno & Rao, 1992; Zhou *et al.*, 1992), however this character is unclear and cannot be unambiguously determined in either taxon owing to preservation (Fig. 5). The absence of an intermetacarpal space in the holotype of *C. yandica* has also been used to distinguish the two taxa but this morphological difference was dismissed as diagenetic by Sereno *et al.* (2002). After reviewing the morphology preserved in IVPP V9769, we concur with the latter interpretation. The preserved morphology is very distinctive and observed among other enantiornithines (e.g., *Rapaxavis, Dapingfangornis sentisorhinus, Hebeiornis*), with the minor metacarpal having a rectangular cross-section, dorsoventrally wider than craniocaudally thick. In fully articulated enantiornithines, the cranial surface of the minor metacarpal is concave so that the size of the intermetacarpal space does not appear the same from dorsal and ventral views. While no space appears present in either carpometacarpus in dorsal view (IVPP V9769a), a small space is clearly visible in ventral view (IVPP V9769b; Fig. 5A). As in other enantiornithines, the minor metacarpal is proximally contiguous with the pisiform process (IVPP V9769b), slightly wrapping around the major metacarpal distally (e.g., *Eoenantiornis buhleri, Hebeiornis, Rapaxavis*; Hou *et al.*, 1999). This morphology is also present in the holotype of *S. santensis* (Fig. 5B). The intermetacarpal space still appears larger in *S. santensis* however this may be due

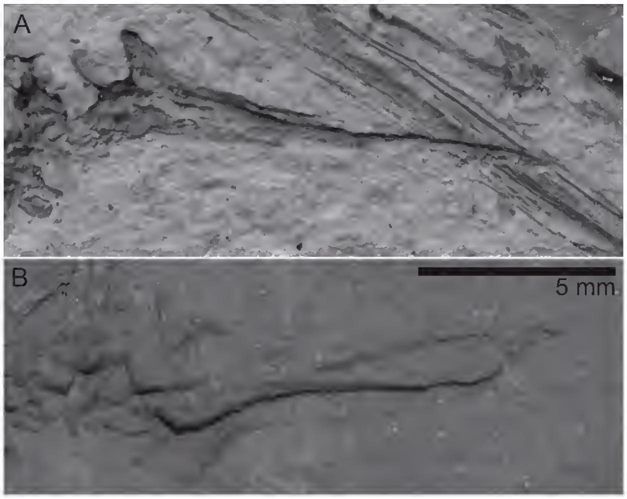

Figure 4. Pygostyle of (*A*) *Cathayornis yandica* (IVPP V9769a); (*B*) *Sinornis santensis* (cast of BNHM BPV 538a). Scale true for A and B.

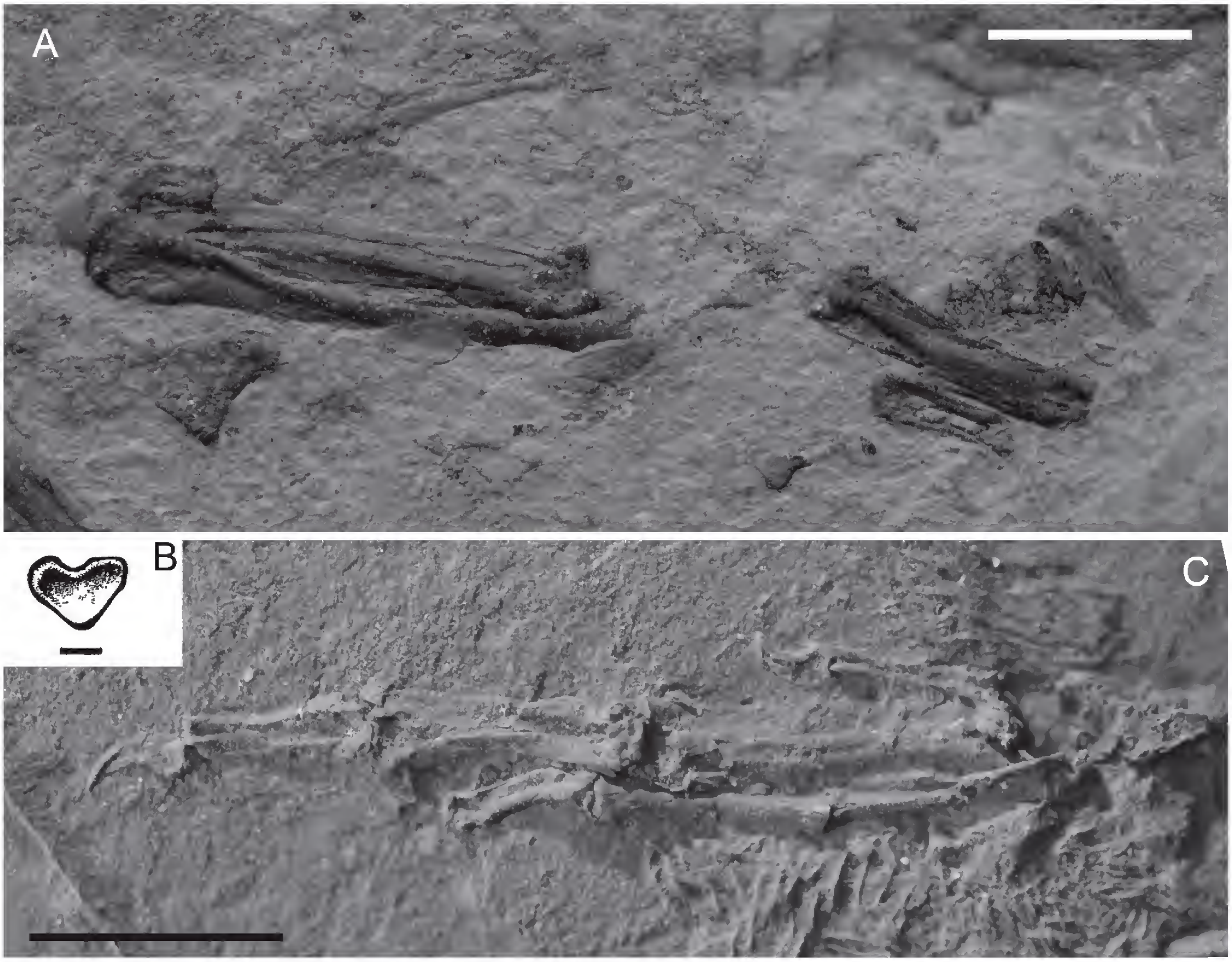

Figure 5. Carpometacarpus of (*A*), *Cathayornis yandica* (IVPP V9769b, left manus); and (*B*), *Sinornis santensis* (cast of BNHM BPV 538a, right manus). Scale bars equal 5 mm.

to the better preservation of the manus (in articulation) in the holotype specimen (Fig. 5B).

Sereno *et al.* (2002) also noted a difference in the relative proportions of the manual claws between the holotypes of *S. santensis* and *C. yandica*, with the major ungual larger than the alular ungual in the former taxon and the two claws subequal in the latter. Zhou & Hou (2002) considered that the alular claw is larger than the major claw in *C. yandica*, with claws of subequal size in *S. santensis*. These different interpretations based on the same specimens result partially from the poor preservation of the manus in *C. yandica* and the very small difference in size that is being considered here. Based on our observations, the manual claws are nearly subequal in both taxa, although the major claw is proportionately larger in *S. santensis* while the alular claw is larger in *C. yandica* (Fig. 5). The two specimens therefore preserve the opposite condition, and this morphological difference, although slight, can be used to distinguish the two taxa.

The morphology of the first phalanx of the minor digit also differs between the taxa. In the holotype of *C. yandica* this phalanx is clearly straight, rectangular to trapezoidal, tapering distally (Fig. 5A) while in *S. santensis* it is curved with a concave ventral margin (Fig. 5B) (Zhou & Hou, 2002). The curved phalanx of *S. santensis* is also proportionately longer than that of the hand of *C. yandica* (Zhou & Hou, 2002). The morphological disparity of this phalanx between the two specimens was noted by Sereno *et al.* (2002) but was dismissed as intraspecific variability. The curvature present in the *S. santensis* holotype is clearly distinct from the straight morphology preserved in the *C. yandica* holotype. Given the differences already noted between the specimens, however, additional specimens of *S. santensis* are required to argue that this curvature is indeed intraspecific variation. Until then, this morphology is considered diagnostic of *S. santensis*.

Pelvic girdle. The pelvic girdle is well-preserved in the holotype of *S. santensis*, nearly complete, fully articulated and missing only the preacetabular wing of the ilium (Fig. 6A). This contrasts with the almost completely disarticulated and incomplete pelvic girdle of the holotype of *C. yandica*. Although both specimens were reported by Sereno *et al.* (2002) to have ischia of similar morphology, this cannot be verified given the poor preservation of this region in the holotype of *C. yandica*. This element was reconstructed by Zhou & Hou (2002); however this information comes from a referred specimen first published by Hou (1997—no collection number). The specimen is an isolated fully articulated pelvis; Zhou & Hou (2002, fig. 7.7H) illustrated the pubis as bent in lateral view, a morphology that cannot be confirmed in *C. yandica* IVPP V9769. With insufficient justification for the assignment of this pelvis to *C. yandica*, information from this specimen is not utilized here pending further investigation.

The ischium of *S. santensis* is consistent with that of other enantiornithines in that it possesses a large proximally located dorsal process but lacks an obturator process (Chiappe &

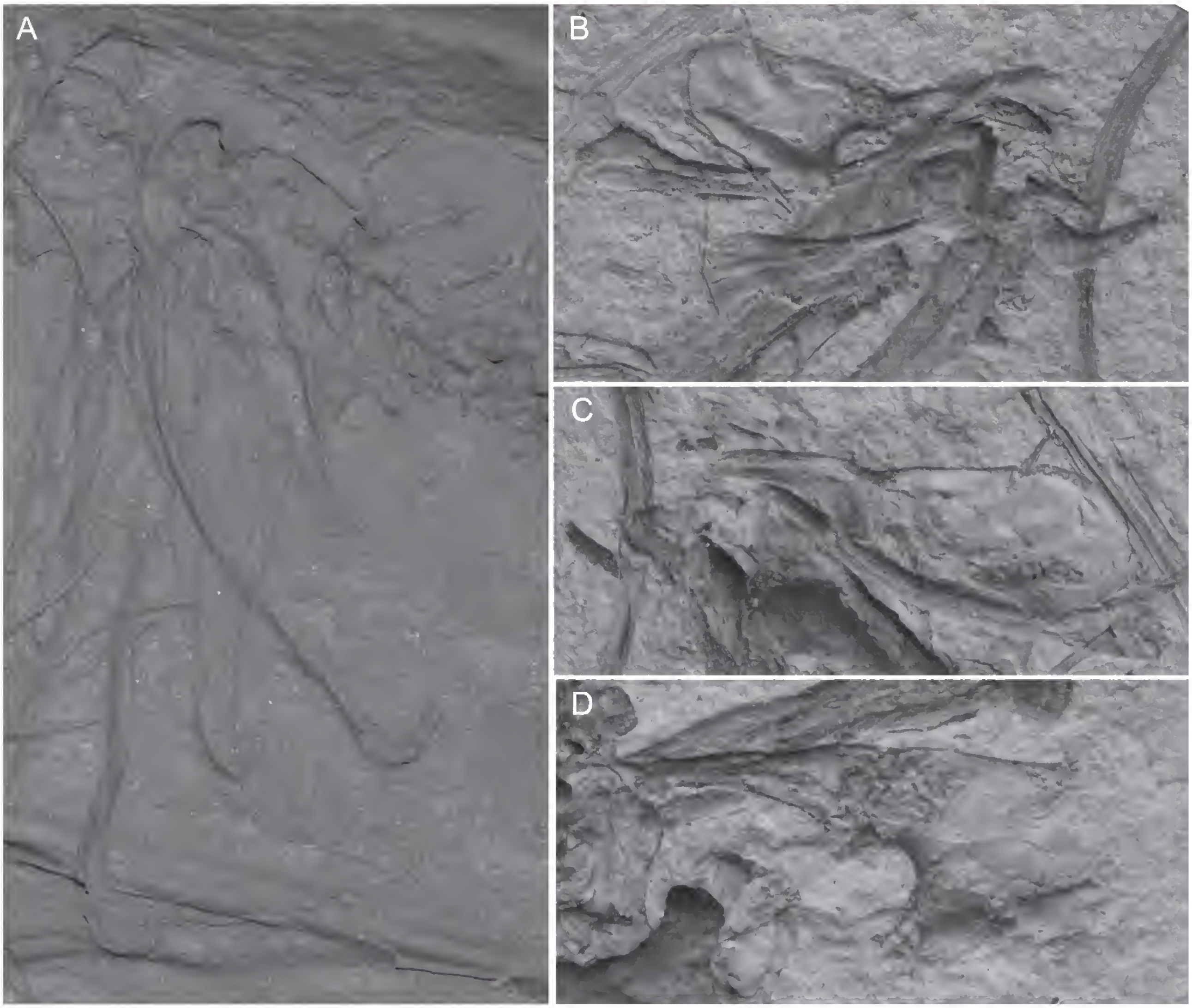

Figure 6. (*A*), cast of the pelvic girdle in *Sinornis santensis* BNHM BPV 538a; (*B*), left ilium of *Cathayornis yandica* IVPP V9769b; (*C*), left ilium IVPP V9769a; (*D*), right ilium IVPP V9769a.

Walker, 2002). The dorsal curvature of the caudal ischium present in the holotype specimen of *S. santensis* is also present in *Eoenantiornis* and clearly distinct from the strap-like ischia present in some other Early Cretaceous Chinese enantiornithines (e.g., *Longipteryx*, DNHM D2950/1). Visible in the cast of the IVPP V9769b is what appears to be the corpus of the ischium preserved overlapping the ilium. While detailed morphologies remain unclear, this bone shows the same dorsal and medial curvature that is present in the *S. santensis* holotype (contra Sereno & Rao, 1992). Given the poor preservation of the ischium in the holotype of *C. yandica*, this morphology is subject to interpretation and cannot be used to align the two species; medial curvature of the ischia is also known in several other enantiornithines (e.g., *Concornis lacustris, Dapingfangornis, Rapaxavis*; Sanz & Buscalioni, 1992).

Cathayornis yandica was described as lacking an antitrochanter on its pelvis while this structure is reportedly present in *S. santensis* (Zhou & Hou, 2002). This difference is also very difficult to determine because of the lack of fusion and complete disarticulation of the pelvic girdle in the holotype of *C. yandica* and the absence of a well-preserved ischium in this specimen; however, because the antitrochanter is typically located just where the ischium and ilium contact, the presence of an antitrochanter cannot be ruled out. A small triangular antitrochanter is clearly present in the holotype of *S. santensis*; the structure is located primarily on the ilium, consistent with other Early Cretaceous enantiornithines (e.g., CAGS-IG-05–CM-06; JOC pers. obs.). This region of the ilium is only visible on the left in the holotype of *C. yandica*, but damaged so that no antitrochanter appears present.

Zhou & Hou (2002) also diagnosed *C. yandica* as having a rim over the craniodorsal margin of the acetabulum; this feature is clearly visible on the holotype of *S. santensis* extending over the entire cranial and dorsal margins of the acetabulum, contiguous with the antitrochanter (Fig. 6A). In *C. yandica* this rim can only be seen on the craniodorsal margin and is cut off where the ilium is damaged so that it cannot be determined if the crest continued and was also contiguous with an antitrochanter, as in *S. santensis*. A supracetabular process (the 'dorsal antitrochanter' of Sereno *et al*., 2002) is also present in both specimens (Fig. 6A,B,C).

Although the ilium in both species is very similar in terms of its general shape and proportions, close comparison of the two specimens reveals additional minor differences in the morphology of the postacetabular wing (Fig. 6). The dorsal margin of this wing of the ilium in *S. santensis* is dorsally convex while the ventral margin is slightly concave so that the

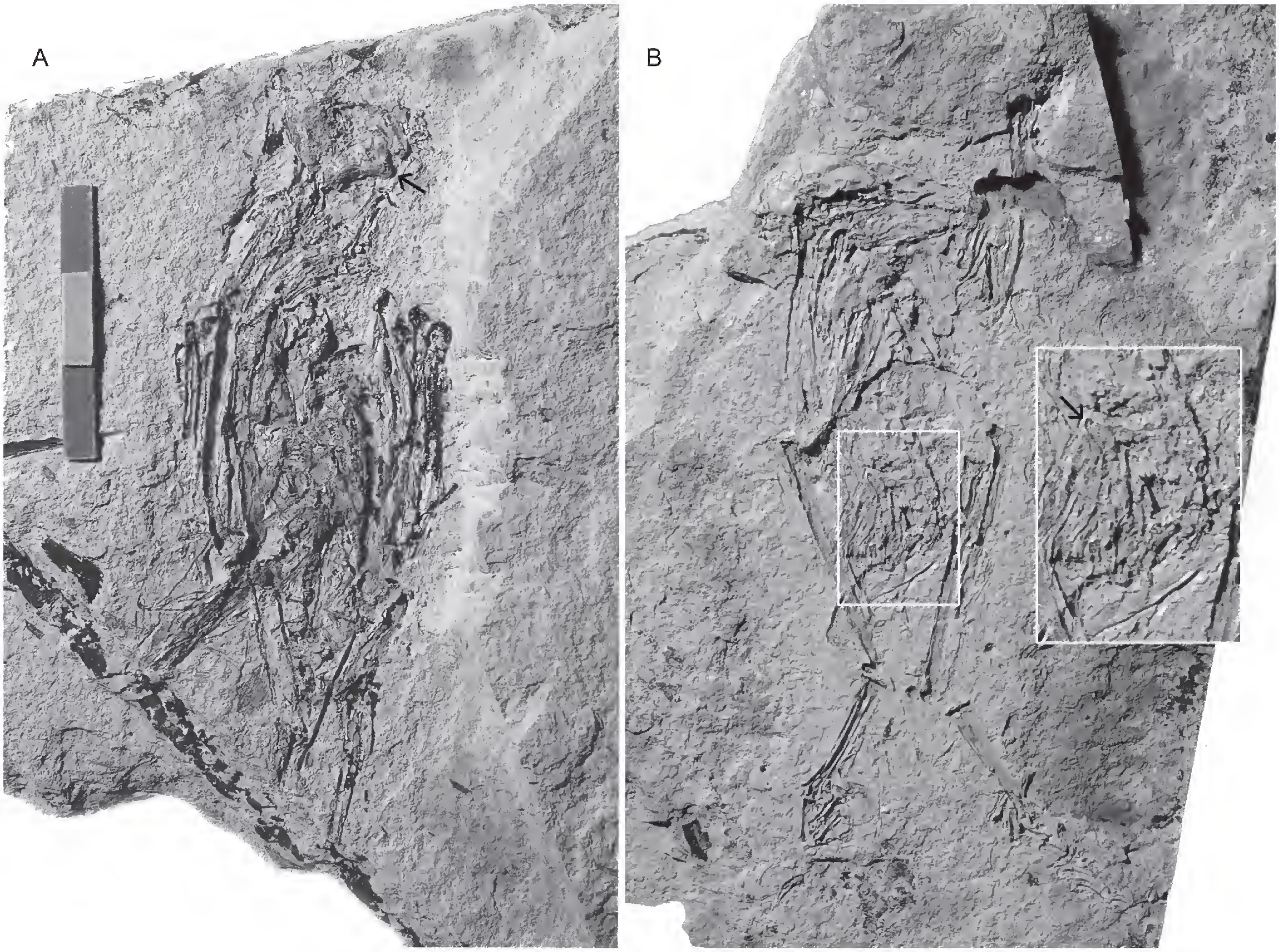

Figure 7. Holotype of (*A*), *Cathayornis aberransis*, IVPP V12353; and (*B*), *Cathayornis caudatus*, IVPP V10917. Scale bar is true for both specimens and totals 30 mm.

entire postacetabular wing is slightly curved in a caudoventral direction (Fig. 6A). The postacetabular blade is thus strongly triangular. In contrast, the left postacetabular process of *C. yandica* has a straight dorsal margin with a ventrally concave ventral margin and is directed caudally (Fig. 6C,D). The process tapers caudally in both specimens but much less in the *C. yandica* holotype, which terminates in a blunt distal margin. In the holotype of *S. santensis* this termination forms a sharper point (Fig. 6A). Overall, the morphology of *C. yandica* is more strap-like than that of *S. santensis* (Fig. 6D).

A three-dimensionally preserved enantiornithine (CAGS-IG-05–CM-06) from the slightly younger Xiagou Formation, Gansu, China, possesses a nearly complete and fully articulated pelvic girdle, and displays the same straight morphology as *C. yandica* (JOC pers. obs.). This results in a difference in the shape of the 'ilioschiadic fenestra' between *S. santensis* and the Xiagou enantiornithine, which suggests that the morphology observed in *C. yandica* is not a preservational artifact but a true difference that can be used to differentiate the two taxa.

Differentiating *S. santensis* and *C. yandica*

After examining the morphologies proposed to either align, or separate, the two specimens, we find significant morphological variation between the two holotypes that we feel justifies maintaining the two as distinct taxa. Preserved characters have been identified, and are supported here, that can be used to formulate a rigorous differential taxonomic diagnosis for the first time.

Sinornis santensis (BNHM BPV 538) differs from *C. yandica* (IVPP V9769) in that: (1) the first phalanx of the minor digit is curved (cf. straight in *C. yandica*) and proportionately longer relative to the first phalanx of the major digit; (2) the claw of the major digit is proportionately larger relative to that of the alular digit; (3) the postacetabular wing of the ilium is proximally broad, curved and tapered distally (cf. 'strap-like' in *C. yandica*); (4) the ulnare is U-shaped with a relatively deep narrow incisure (wide and shallow incisure in *C. yandica*) and; (5) the pygostyle is shorter (¾ the length of that of *C. yandica*).

Referred specimens of *Cathayornis yandica*. A number of specimens have been referred to *C. yandica* both in publications and informally in small museums around China (Martin & Zhou, 1997; Hou, 1997; Hou *et al*., 2002; Zhou & Hou, 2002; JOC, pers. obs.). Indeed, many of these specimens preserve regions of the skeleton poorly known in the holotype, such as an articulated pelvic girdle (Hou, 1997, fig. 54, p. 136, no collection number) and hindlimbs (IVPP V9936, Zhou & Hou, 2002; IVPP V10533, V10904, Hou, 1997) that offer the possibility of further comparison with *S. santensis* and additional morphological differentiation if correctly assigned. For example, both *C. yandica* and *S. santensis* have a plantarly excavated tarsometatarsus formed by keel-like medioplantar and lateroplantar margins of metatarsals II and IV respectively, a morphology observed in a number of enantiornithines (e.g., avisaurids). Although the distal ends of the metatarsals in *C.*

yandica are not preserved in the holotype specimen, a well preserved referred specimen IVPP V9936 reveals that the metatarsals of these birds are arranged in a single horizontal plane while the trochlea of metatarsals II and IV of *S. santensis* (visible in the holotype specimen) are displaced plantarly. However, because the morphological information comes from an unconfirmed referred specimen, this cannot yet be considered a true diagnostic character of *C. yandica*. The small overall size and subtly of the morphological differences between these birds suggest that only a complete and detailed inspection of all referred specimens will determine their taxonomic assignment. Pending such a revisionary study, it is recommended that referred specimens should not be used to supplement data from the holotype or used with extreme caution.

Cathayornis aberransis, C. caudatus and C. chabuensis. Although we have presented an argument in favor of the validity of *C. yandica*, this alone does not completely clarify the taxonomic status of the genus. Three other species have to date been assigned to *Cathayornis*; the validity of two species is variably accepted, while the third has only recently been described (*C. chabuensis*—Li *et al.*, 2008). Although *C. caudatus* and *C. aberransis* have been considered invalid by some (Sereno *et al.*, 2002; Zhou & Zhang, 2006), the only published record of this was not corroborated by morphological evidence (Zhou *et al.*, 2008b). These two taxa, and three others (*Longchengornis sanyanensis, Cuspirostrisornis houi*, and *Largirostrornis sexdentornis*; Hou, 1997) have been synonymized under *C. yandica* based on the fact the holotype specimens of these taxa were all collected from the same locality, despite the presence of morphologies distinct from *C. yandica* in some specimens (e.g., *Longchengornis*, Zhou *et al.*, 2008b). This suggests a careful taxonomic review of these poorly preserved specimens was not conducted. Accordingly, the taxonomy of *C. aberransis* and *C. caudatus* is revisited here. The taxonomic status of these taxa is discussed individually and with caution; the specimens were not accessed first hand so their validity and anatomy is evaluated from published data. However, we argue that this should be adequate: if published data are not sufficient to differentiate a new species from known taxa, then it does not add to our knowledge of the clade, or facilitate future research; a specimen affixed to a name in this way, although unique, still represents a *nomen dubium.*

Cathayornis aberransis. Known from a single specimen, IVPP V12353 (Fig. 7A), *C. aberransis* comes from the Jiufotang Formation of northeastern China (Hou *et al.*, 2002); the specimen was studied from published photos of the slab and counterslab (Hou *et al.*, 2002; Hou, 2003). This taxon was diagnosed by the presence of a crest between the two frontals with processes on the frontal sides (tubercles), numerous teeth in the maxilla, a distally developed sternal carina, sternal outer trabeculae distally ending proximal to the distal end of the xiphoid process ("sternum lateral process no longer than posterior process"), a humerus that is shorter than the ulna, and a distally fused pubis (Hou *et al.*, 2002). Most of these diagnostic characters are weak because they are widely distributed amongst Mesozoic birds, while some (humerus shorter than ulna, presence of teeth in the maxilla, a distally contacting pubis) are plesiomorphic to Ornithothoraces (O'Connor *et al.*, 2009). The morphology of the sternum in IVPP V12353 cannot be confirmed and the distal ends of the pubes are clearly non-contacting and thus, while likely joined in a symphysis in life (evident from their expanded distal ends), the pubes were not fused (*contra* Hou *et al.*, 2002). The frontals are fairly well preserved in dorsal view, whereas typically enantiornithine frontals are preserved in lateral view. A longitudinal ridge appears absent; the frontals are unfused and the slight medial separation of the two bones may have been interpreted as a ridge. The caudolateral corner of the frontals project ventrolaterally, presumably for articulation with the postorbital and squamosal bones (Fig. 7A). Given the dorsal view, this feature may be exaggerated in *C. aberransis*, however because it cannot be readily compared in terms of exact size and shape to other enantiornithines (visible in lateral view in *Pengornis, Rapaxavis*, LP 4450, GMV 2159, DNHM D2567), this process and morphology are accepted as possibly diagnostic characteristics for this taxon.

While there exists published data supporting the validity of this taxon, albeit weakly, much of the published information has also been shown to be inaccurate and thus studies that incorporate this species must be cautious. Further preparation followed by detailed study is required to verify the validity of this specimen.

Cathayornis caudatus. The holotype and only known specimen of *C. caudatus*, IVPP V10917 (Fig. 7B), also comes from the Jiufotang Formation, Liaoning, China (Hou, 1997, 2003; Hou *et al.*, 2002). The taxon is diagnosed as a small *Cathayornis* species with a transverse groove between the frontal and parietal, more than three teeth in the dentary, a well-developed sternal carina, an elongate tarsometatarsus more than half the length of the tibiotarsus, and a short bony tail lacking a pygostyle (Hou, 1997). A toothed dentary and sternum with carina are plesiomorphic to Enantiornithes (Chiappe & Walker, 2002); based on the relative lengths of the femur and tibiotarsus, IVPP V10917 is only 2–5% smaller than *C. yandica* (IVPP V9769), so the new specimen is essentially the same size as other *Cathayornis*. Given the poor preservation of the hindlimb in the holotype of *C. yandica*, the length of the tarsometatarsus relative to the tibiotarsus cannot be accurately compared between the two taxa. No transverse groove or comparable structure on the frontal, which is preserved in lateral view, can be identified from photographs. A fully fused pygostyle of typical enantiornithine morphology (appears forked dorsally and to have possessed a laterally projected flange) is clearly visible in one of the slabs (Hou, 1997; Hou *et al.*, 2002; counterslab in Hou, 2003) overlapping the sternum and pelvic elements (Fig. 7B). The free caudal vertebrae illustrated by Hou (1997) are reinterpreted as the proximal portion of the left pubic shaft. Although currently available published data fail to support the validity of this taxon, further preparation and study of IVPP V10917 may identify unique morphologies that support *C. caudatus* as a valid taxon. Until this time, this taxon is regarded as a *nomen dubium.*

Cathayornis chabuensis. The holotype of *C. chabuensis*, BMNHC Ph000110ab, greatly extends the known geographical range of cathayornithiforms (Zhou & Zhang, 2006); the specimen comes from exposures of the Jingchuan Formation at the Chabu Sumu locality near Otog Banner, in the northwest of the Otog basin, Inner Mongolia, China (Li *et al.*, 2008). The specimen is assigned to *Cathayornis* on the basis of a longitudinal groove on the dorsal surface of the radius, a narrow intermetacarpal space, and a minor digit formed by single phalanx that closely abuts the first phalanx of the major digit (Li *et al.*, 2008). This suite of morphologies does not diagnose *Cathayornis* or even distinguish it from other enantiornithines and thus this taxonomic assignment is unsubstantiated. The presence of a longitudinal groove on the radius is a synapomorphy of a subclade of enantiornithines (Chiappe & Walker, 2002). Most enantiornithines have a minor digit formed by two phalanges, both of which are reduced, the second often to a very small fragment less than 10% the size of the first phalanx (e.g., *Eoalulavis lacustris, Longipteryx, Rapaxavis*; Sanz *et al*., 1996); a second phalanx was likely present in BMNHC Ph000110ab, but may not have been preserved given the disarticulated and incomplete nature of the specimen and the very small size of this phalanx.

The specimen is distinguished from *C. yandica* by the slightly greater lateral projection of the outer (lateral) sternal trabeculae, as well as the relatively more caudal extension of the keel (Li *et al*., 2008). Although the quality of published photographs and illustrations makes it difficult to verify these anatomical details given that the keel is not visible and the very minimal degree of lateral splay of the outer sternal trabeculae that is being compared, the specimen was available for study and these differences have been verified. The more caudal extension of the keel, however, is here interpreted to refer to the caudal extension of the xiphial region (xiphoid process) relative to the outer sternal trabeculae; the outer trabeculae end proximal to the caudal xiphial margin (as in *Elsornis keni, Shanweiniao cooperorum*; Chiappe *et al*., 2006; O'Connor *et al*., 2009), as opposed to some enantiornithines in which the two processes end at approximately the same level (e.g., *Longipteryx, Protopteryx fengningensis*; Zhang & Zhou, 2000) or the outer trabeculae extend beyond the xiphoid process (e.g., *Concornis, Rapaxavis*). Another apparent distinction between the two species, a well-developed distal expansion appears absent from the outer sternal trabeculae, whereas *C. yandica* has large asymmetrical fan shaped expansions (also present in *C. caudatus*). The new specimen is further distinguished from previously identified specimens of *Cathayornis* by its locality, which is over 1000 km away from Chaoyang, Liaoning, where other *Cathayornis* specimens have been collected. Although this specimen is considered distinct from *C. yandica*, the characters used to assign this specimen to the cathayornithiforms are unsupported. With limited preserved material for comparison in the holotype of *C. chabuensis*, the taxonomic assignment of this species may have to await additional discoveries or a better understanding of Cathayornithiformes.

Discussion

Here we have provided a comprehensive overview of the taxonomic issues regarding *Cathayornis yandica* and *Sinornis santensis*, as well as the less prominent issues of specimens and species assigned to the former. The latter issues may not be as apparent in the literature and thus to the international scientific community, but they represent problems that extrapolate outwards from a single taxonomic issue into many. Taxonomic research, although seemingly mundane, is of great significance and importance to the scientific community. Without sound taxonomy, the results of research can be obscured by synonymous taxa and misidentified specimens. Without rapid rectification of old problems, new taxonomic issues will arise and spread throughout the literature. Taxonomic consistency and accuracy provides a sound base for future research within an international community, facilitating common understanding and cooperative research. While old taxonomy will inevitably require revision, as seen with *C. yandica* and *S. santensis*, some revisions do not necessarily clarify issues or produce consistency. The aim of this review was not only to try to resolve this issue and increase future taxonomic consistency between Mesozoic bird researchers, but also to address the reasons why such taxonomic revisions are often necessary.

Vertebrate paleontology is a science that will always be plagued with doubts, assumptions, and missing data. Our knowledge of taxa and their morphology is limited by available fossil material, compromised by the processes of death, fossilization, and diagenesis. It has long been understood that the naming of vertebrate fossil taxa is especially subjective because diagnostic characteristics can be based only on preserved morphology, which can be interpreted differently among workers (Amadon, 1963; Cracraft & Eldredge, 1979): one person examining a fossil may view it as 'considerably different' in morphology compared to someone else. The proliferation of potential synonyms, homonyms and *nomina dubia* has been especially evident in the study of Mesozoic birds as recent years have seen an explosion in the numbers of known fossils leading to an exponential rise in the number of named taxa since the mid-1990s (Fountaine *et al*., 2005; Chiappe & Dyke, 2007). While the need for taxonomic revision is not unique to the enantiornithine clade, nor can it ever be avoided entirely, it is observed that in this clade, a majority of these problems arise as a result of (1) the use of inadequate, fragmentary and undiagnostic holotype material (resulting in *nomina dubia*—taxa that cannot be distinguished from others, e.g., *C. caudatus*); (2) inadequate comparisons of new taxa with those already described (resulting in the subsequent erection of junior synonyms); (3) differences in interpretation of fossils (perhaps based on observed morphological differences or via a taphonomic effect); and (4) variation in species definitions (basing a new taxon on the fact that it comes from a different locality to other similar forms).

The well-known Chinese fossil enantiornithine birds *Cathayornis yandica* and *Sinornis santensis* are both represented by fairly complete specimens yet there has been debate over their status as distinct taxonomic entities. Largely this debate has occurred because clear diagnostic characters had not been presented in the original descriptions, which appeared simultaneously, preventing comparison. However later publications continued to differ on this matter as a result of differential interpretation of preserved morphologies and their significance. Close inspection reveals important morphological differences indicating that these two taxa are clearly distinct from one another and should remain separate taxa. Assigned species of *Cathayornis* remain ambiguous from published data, suggesting that the ability to differentiate and diagnose IVPP V9769 and BNHM BPV 538 may be in large part due to their preparation. In these specimens, bones were removed to create clean voids and moulds and casts were made for study so that the maximum amount of data could be retrieved from each specimen. Despite the fact new species were erected from these specimens, preparation is largely absent in the holotypes of *C. caudatus* and *C. aberransis*, making it difficult to clearly establish morphological differences. Casts were made of BMNHC Ph000110ab, and *C. chabuensis* can be distinguished from other known taxa (Li *et al*., 2008).

While disagreements about taxonomic validity and the interpretation of a given morphology result in new ideas and stimulates research, the erection of taxa based on fragmentary materials without a clear diagnosis serves only to slow the progress of research into a given clade. Despite the system of peer review and its intended purpose, large numbers of taxa of fossil birds have been described with inadequate diagnoses (Hou, 1997; Li *et al.*, 2006). When a taxon lacks an accurate diagnosis, the validity of the taxon is questioned making the species a potential *nomen dubum*. With the global distribution of Enantiornithes in mind, individual access to every specimen is unlikely and thus publications must include important and pertinent data so that there is no question regarding the species validity. In the case of *C. aberransis* and *C. caudatus*, the morphological features cited in the published diagnoses for these species could nearly all either be invalidated from the photographic data or are not diagnostic features (plesiomorphies). Furthermore, preservation and the quality of preparation and published photographs prevent independent detailed morphological inspection and the identification of autapomorphies. Because the publications are uninformative, these taxa become functional *nomina dubia*.

Others species have been described based on specimens in private collections, unavailable to the scientific community, and thus rendering any interesting data they may have to contribute unverifiable and useless (*Dalingheornis liwei*; Zhang *et al.*, 2006). The most recent example of this worrying trend is the description of a new, small enantiornithine bird from the Crato Formation of Brazil (Naish *et al.*, 2007), potentially the oldest fossil bird known from Gondwana (Close *et al.*, 2009), but held in a private colletion.

The biggest problem of all, however, is the erection of taxa based on largely incomplete specimens (Table 1; e.g., *Explorornis nessovi, Lectavis bretincola, Martinavis cruzyensis*; Panteyelev, 1998; Chiappe, 1993; Walker *et al.*, 2007). Over a third of all known enantiornithines are named from bone fragments (less than a single whole bone); these specimens may be interesting to the scientific community because they extend a temporal or geographic range, but their existence as distinct taxa is unjustifiable given the inability to compare the specimens to a majority of known taxa and specimens. For whatever reason scientists are compelled to erect taxa from fragmentary material, it is up to the scientific community as reviewers to prevent undiagnosible or comparable specimens from being named. When taxa are based on private material, or are for other reasons invalid, the scientific community should unify in excluding these 'taxa' when discussing the clade they are purported to belong to. This will hopefully discourage the continued practice of the erection of such taxa (e.g., *Dalingheornis*, Zhang *et al.*, 2006). While it is very important to describe new material, erecting a new genus based on a bone fragment or publishing information that can never be verified does little to help clarify enantiornithine diversity and relationships.

Conclusions

Differences will always exist in preferred taxonomic requirements; differences in opinion lead to new investigations, and ultimately greater knowledge. However if a proposed new taxon serves only to increase ambiguity within the taxonomy of a clade, then we urge editors and reviewers to reject such research. The peer review system is in place to ensure that published data maintains a certain level of quality. This is to protect the integrity of published data and facilitate future research. Species based on highly fragmentary material, unprepared materials, or private collections should be rejected. Any publication that does not adequately document a new taxon should be subject to revision so that additional publications on the morphology of a single specimen are not required. In the cases of *Cathayornis yandica* and *Sinornis santensis*, the original publications appeared simultaneously preventing comparison at the time and the similarity of the species necessitated further review. In the cases of *C. aberransis* and *C. caudatus*, the original publications fail to provide valid arguments for the erection of new species, and have thus made revisionary research absolutely necessary. After reviewing these issues, the morphological differences between the holotypes of *Cathayornis yandica* and *Sinornis santensis*, some already noted by Sereno *et al.* (2002) and Zhou & Hou (2002), are utilized to distinguish the two taxa. Because of similarities between these taxa, future identifications of morphologically comparable specimens require detailed study to prevent the need for further revision.

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A New Avian Species with Tubercle-bearing Cervical Vertebrae from the Middle Eocene of Messel (Germany)

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ABSTRACT. A new avian species, *Perplexicervix microcephalon* n.gen. and n.sp., is described from the Middle Eocene of Messel in Germany. It is most unusual in that the cervical vertebrae of five of the six known specimens bear numerous bony tubercles. Such tubercles were also reported from another avian fossil from the Messel deposits, which is a representative of the extinct taxon Idiornithidae. Although the osteology of *P. microcephalon* is not known well enough for a reliable phylogenetic assignment, the new species clearly does not belong to the Idiornithidae. Compared to extant birds, it agrees with Anhimidae and Cathartidae in some osteological features. The origin of the vertebral tubercles remains mysterious. The fact that these structures are now known from two unrelated avian taxa supports previous assumptions, that they represent a pathologic condition. Not in line with this assumption, however, is their occurrence in all specimens referred to *P. microcephalon*, in which cervical vertebrae are preserved.

MAYR, GERALD, 2010. A new avian species with tubercle-bearing cervical vertebrae from the Middle Eocene of Messel (Germany). In *Proceedings of the VII International Meeting of the Society of Avian Paleontology and Evolution*, ed. W.E. Boles and T.H. Worthy. *Records of the Australian Museum* 62(1): 21–28.

Peters (1995) described a remarkable skeleton of a large bird from the Middle Eocene of Messel in Germany as *Idiornis tuberculata*. This species belongs to the Idiornithidae, stem lineage representatives of the Cariamidae. Apart from being the most complete skeleton of an idiornithid, it is of particular interest in that the cervical vertebrae and few other bones are covered by numerous small tubercles of enigmatic origin and significance.

Such tubercles were subsequently also reported on the cervical vertebrae of two other bird specimens from Messel, and on a cervical vertebra from the Quercy fissure fillings in France (Mayr, 2007). Both Messel fossils consist only of skulls with a few cervical vertebrae, and belong to a bird that is smaller than *I. tuberculata*. Because of their fragmentary preservation, a taxonomic and phylogenetic assignment was not possible. Concerning the origin of the tubercles, Mayr (2007) concluded that they most likely are of pathologic origin and document a Paleogene avian disease without a modern counterpart.

Here I describe new fossil birds from Messel which can be referred to the same species as the above-mentioned skulls. One of them is a fairly complete skeleton that was unknown to me in 2007, and has the cervical vertebrae and few other bones likewise covered with numerous small tubercles.

Material and methods

Osteological terminology follows Baumel & Witmer (1993). Measurements are in millimetres and indicate the maximum length of the bone along its longitudinal axis; the length of the claws was measured from the tip of the tuberculum extensorium to the apex phalangis. Institutional abbreviations: SMF—Forschungsinstitut Senckenberg, Frankfurt am Main; HLMD—Hessisches Landesmuseum, Darmstadt.

Systematic paleontology

Neognathae incertae sedis

Perplexicervix n.gen.

Type species. *Perplexicervix microcephalon* n.sp.

Diagnosis. *Perplexicervix* n.gen. is characterized by the following features: (1) skull small in comparison to postcranial skeleton; (2) beak short, triangular in dorsoventral view, with a straight culmen, sigmoid tomia, and a slightly hooked tip; (3) surface of cranium with marked pores and furrows; (4) well-developed processus basipterygoidei present; (5) processus extensorius of carpometacarpus prominent and with broadly rounded tip; (6) tarsometatarsus elongate with short trochleae metatarsorum II et IV; (7) hallux long. Characters (2), (3), and (5) are considered autapomorphies of the new taxon.

Etymology. From *perplexus* (Lat.): incomprehensible, and *cervix* (Lat.): neck, in reference to the curious tubercles on the cervical vertebrae.

Perplexicervix microcephalon n.gen. and n.sp.

Holotype. SMF-ME 11211a+b (partially dissociated skeleton lacking the left leg; Fig. 1a).

Referred specimens. SMF-ME 3548 (skull with atlas, axis, and third vertebra; Fig. 2a), SMF-ME 10846a+b (skull and cranialmost six cervical vertebrae; Fig. 2c), SMF 2559a+b (partial postcranial skeleton; Fig. 3), HLMD-Me 14996a+b (postcranial skeleton; Fig. 1b). There is a further, uncatalogued skeleton of *Perplexicervix microcephalon* in the collection of B. Pohl (Groß-Bieberau, Germany), which also exhibits numerous tubercles on the cervical vertebrae (Fig. 4).

Type locality and horizon. Messel near Darmstadt, Germany; lower Middle Eocene (MP 11; about 47 Ma).

Diagnosis. As for genus.

Measurements. SMF-ME 11211a+b (holotype): Skull, 56.6; humerus ca. 73 (right; visible through the transparent reverse of the slab); ulna, ca. 85 (right), 79.5 (right); carpometacarpus, 40.5 (left), ca. 40 (right); femur, 45.2 (right); tibiotarsus, ca. 71 (?) (right; calculated by adding the lengths of the two broken halves); tarsometatarsus, ca. 60 (?) (right; calculated by adding the lengths of the two

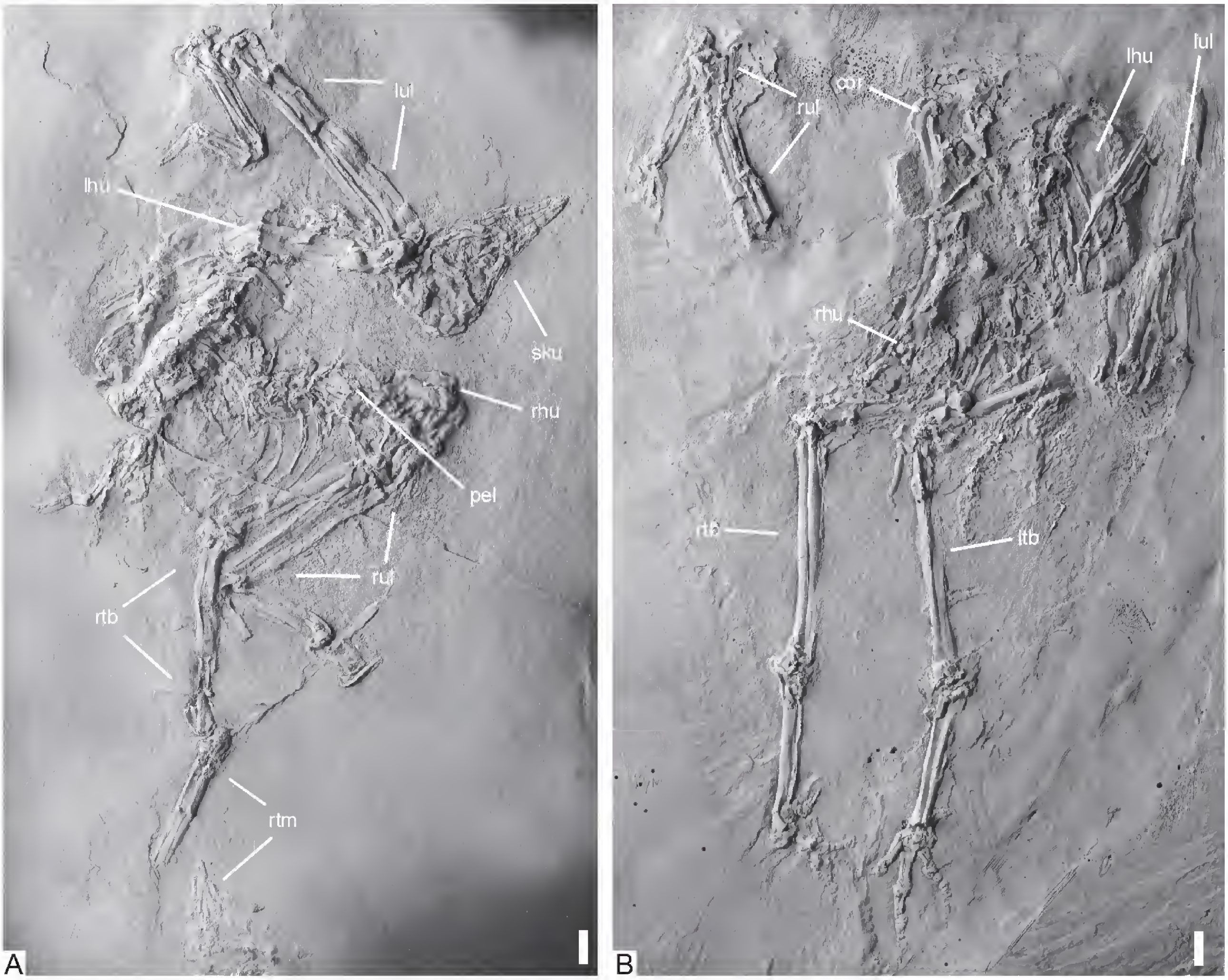

Figure 1. *Perplexicervix microcephalon* n.gen. and n.sp. (*A*) holotype (SMF-ME 11211a); (*B*) HLMD-Me 14996a. Abbreviations: *cor*—coracoid, *lhu*—left humerus, *ltb*—left tibiotarsus, *lul*—left ulna, *pel*—pelvis, *rhu*—right humerus, *rtb*—right tibiotarsus, *rtm*—right tarsometatarsus, *rul*—right ulna, *sku*—skull. Coated with ammonium chloride to enhance contrast; scale bars equal 10 mm.

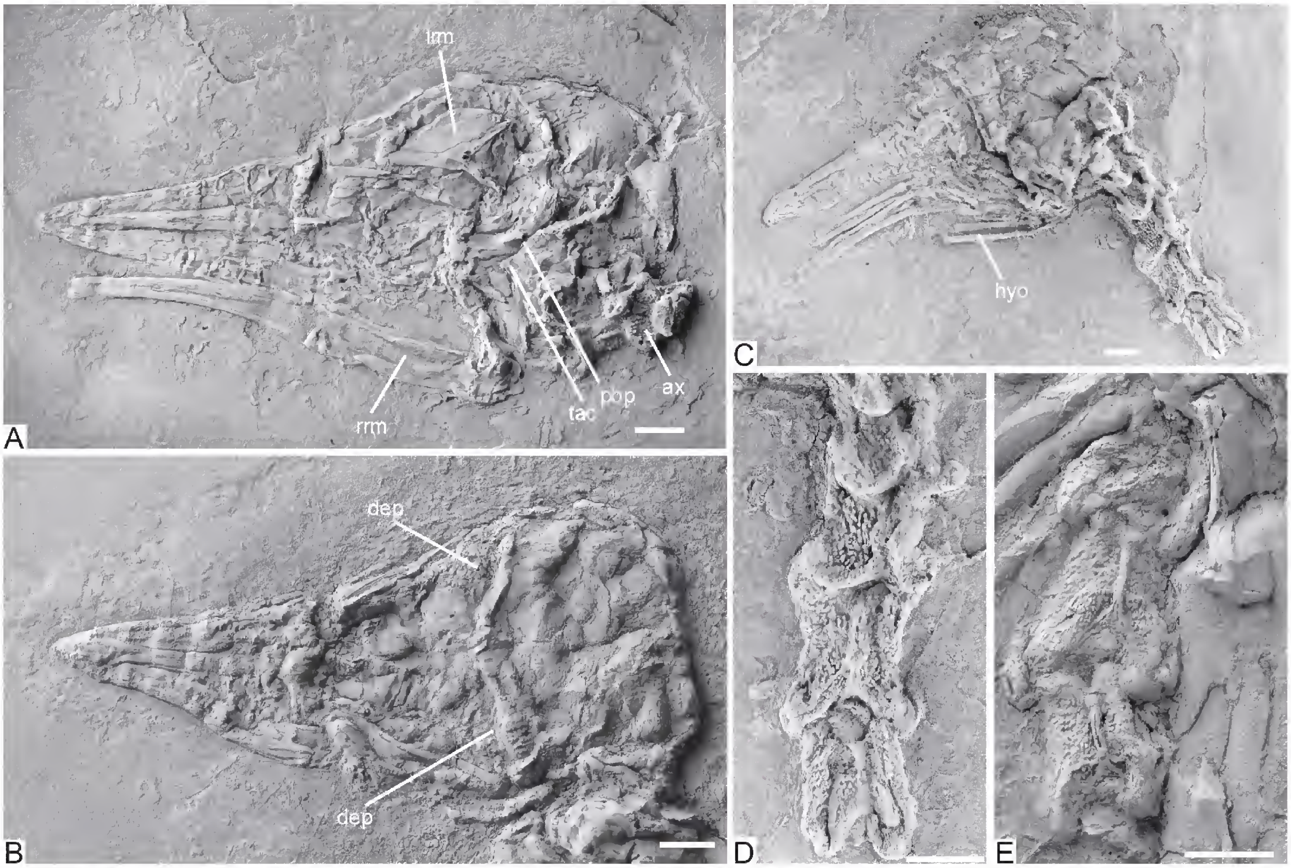

Figure 2. *Perplexicervix microcephalon* n.gen. and n.sp., skull (*A–C*) and cervical vertebrae (*D, E*). (*A*) SMF-ME 3548 (ventral view); (*B*) holotype (SMF-ME 11211a; dorsal view); (*C*) SMF-ME 10846a (lateral view); (*D*) holotype (SMF-ME 11211a); (*E*) referred specimen SMF-ME 10846a. Abbreviations: ax—axis, dep—depressions on cranium (see text), hyo—hyoid bone, lrm—left ramus mandibulae, pbp—processus basipterygoideus, rrm—right ramus mandibulae, tac—tuba auditiva communis. Coated with ammonium chloride to enhance contrast; scale bars equal 5 mm.

broken halves); pedal phalanges: I1, ca. 11.0. SMF 2559a+b: humerus, 80.9 (left); ulna, 84.0 (left); carpometacarpus, 43.0 (left); tibiotarsus, ca. 74.7 (left), ca. 81.0 (right). HLMD-Me 14996a+b: humerus, ca. 80.5 (left), ca. 82 (right); ulna, ca. 85–87 (right); carpometacarpus, ca. 43.5 (right); femur, ca. 46.5 (left), ca. 45 (right); tibiotarsus, ca. 75.5 (left), ca. 75.5 (right); tarsometatarsus, ca. 52 (left), ca. 51.5 (right); pedal phalanges (HLMD-Me 14996a): I1, ca. 12.5 (right); I2, ca. 5 (right); II1, ca. 13.5 (?) (left); III1, ca. 13 (left); III2, ca. 8.5 (left); IV1, ca. 6.5 (?) (left); IV2, ca. 4.5 (left). Pohl specimen: Skull, ca. 61; humerus, ca. 73 (left), ca. 80 (right); ulna, 86.5 (right); carpometacarpus, 40.2 (left); tibiotarsus, ca. 73 (right); tarsometatarsus ca. 51.5 (right). SMF-ME 10846a: Skull, 56.5. SMF-ME 3548: Skull, 66.5.

Etymology. Derived from *micro* (Gr.): small, and *cephalon* (Gr.): head, in reference to the small skull of the new species.

Description and comparisons

As in the Anhimidae (Anseriformes), Galliformes and Columbiformes, the skull is very small in relation to the body. It is also of similar overall proportions to the skull of the Anhimidae and, in dorsal view, becomes gradually narrower towards the tip of the beak. The beak itself is short and, in dorsal view, has a triangular shape. In lateral view (SMF-ME 10846a), it is rather low dorsoventrally, with a straight culmen, sigmoid tomia, and a slightly hooked tip. The narial openings are very long and almost reach into the tip of the beak. The ossa maxillaria are widely separated.

The ventral surface of the skull is exposed in SMF-ME 3548. In this specimen well-developed processus basipterygoidei can be discerned which resemble those of the Cathartidae. The caudal wall of the cavum tympanicum forms a cone-like projection, just caudal to the alae parasphenoidales (SMF-ME 3548), which indicates that the fossa parabasalis, i.e., the depression in which the ostia canalis carotici et ophthalmicus externus are located, was laterally open. Also in SMF-ME 3548, a tuba auditiva communis can be discerned and the lamina parasphenoidalis bears marked pores. As noted previously (Mayr, 2007), there are some low and blunt bony tubercles on the basicranium of SMF-ME 3548. The processus parasphenoidales laterales are well developed.

Perplexicervix microcephalon lacks processus supraorbitales. In the holotype, the dorsal surface of the cranium appears to be elevated caudal of the orbitae, and is contrasted from the rostral portion by a distinct, V-shaped step (Fig. 2b). Although this may be an artifact of preservation, the symmetry of this feature rather indicates that it reflects the true morphology of the cranium, i.e., that either the caudal portion of the cranium was unusually elevated or the rostral

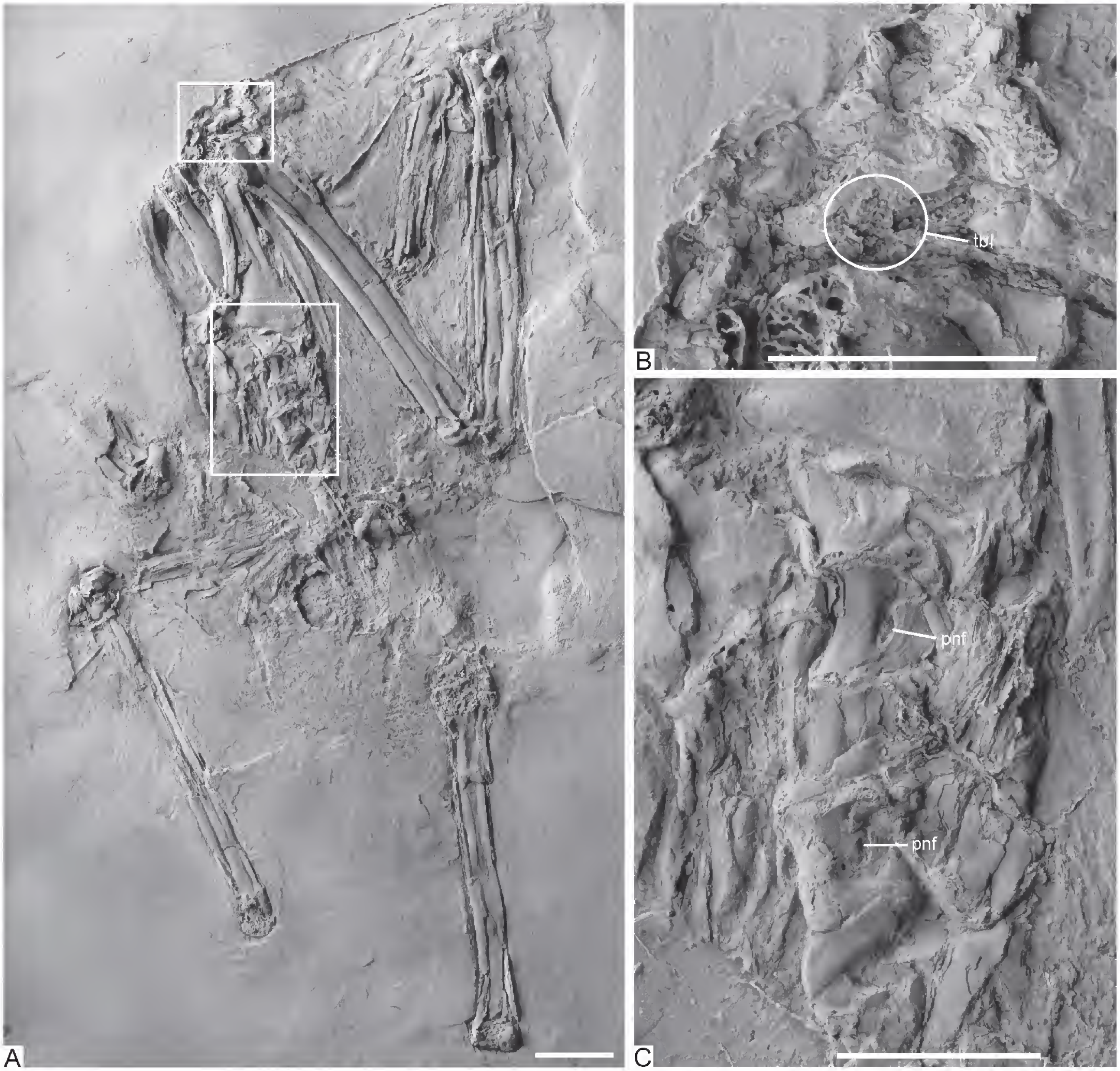

Figure 3. *Perplexicervix microcephalon* n.gen. and n.sp. (*A*) referred specimen SMF-ME 2559a, the framed areas indicate the details shown in *B* and *C*; (*B*) detail of cervical vertebrae; (*C*) detail of thoracic vertebrae. Abbreviations: *tbl*—tubercles on cervical vertebrae, *pnf*—pneumatic foramen. Coated with ammonium chloride to enhance contrast; scale bars equal 10 mm.

portion depressed. In all specimens, the surface of the cranium exhibits large pores and marked furrows (see also Mayr, 2007).

The processus postorbitalis is short, the processus zygomaticus wide, square, and with a truncated tip as in Cathartidae. As far as this can be discerned in the crushed skulls, the fossae temporales appear to have been shallow.

In SMF-ME 3548 the processus oticus of the left quadratum can bee seen in cranial view (Mayr, 2007: fig. 2a), whereas only a small portion of the capitulum oticum of the right quadratum is visible. The processus oticus resembles that of the White-tailed Kite *Elanus leucurus* (Accipitridae); as in the latter, the articulation facet of the capitulum oticum extends onto the cranial surface of the processus oticus. The incisura intercapitularis is very shallow.

The rami mandibulae are dorsoventrally narrow and particularly slender in their distal half; the pars symphysialis (visible through the reverse of the transparent slab of SMF-ME 11211a) is very short, its length is about equal to the depth of the narrow distal section of the rami mandibulae. Fenestrae mandibulae are absent. The caudal part of the mandible bears a well-developed processus medialis.

The cervical vertebrae of section II of Boas (1929) are long and exhibit shallow lacunae interzygapophysiales and elongate, ridge-like processus spinosi (SMF-ME 10846a). At least the fourth cervical vertebra lacks an osseous bridge from the processus transversus to the processus articularis caudalis (arcus interzygapophysialis of Livezey & Zusi, 2006:133) (SMF-ME 10846a). Whether this bridge was present on the third cervical vertebra cannot be clearly discerned (SMF-ME 10846a)—if it was, the enclosed foramen must have been

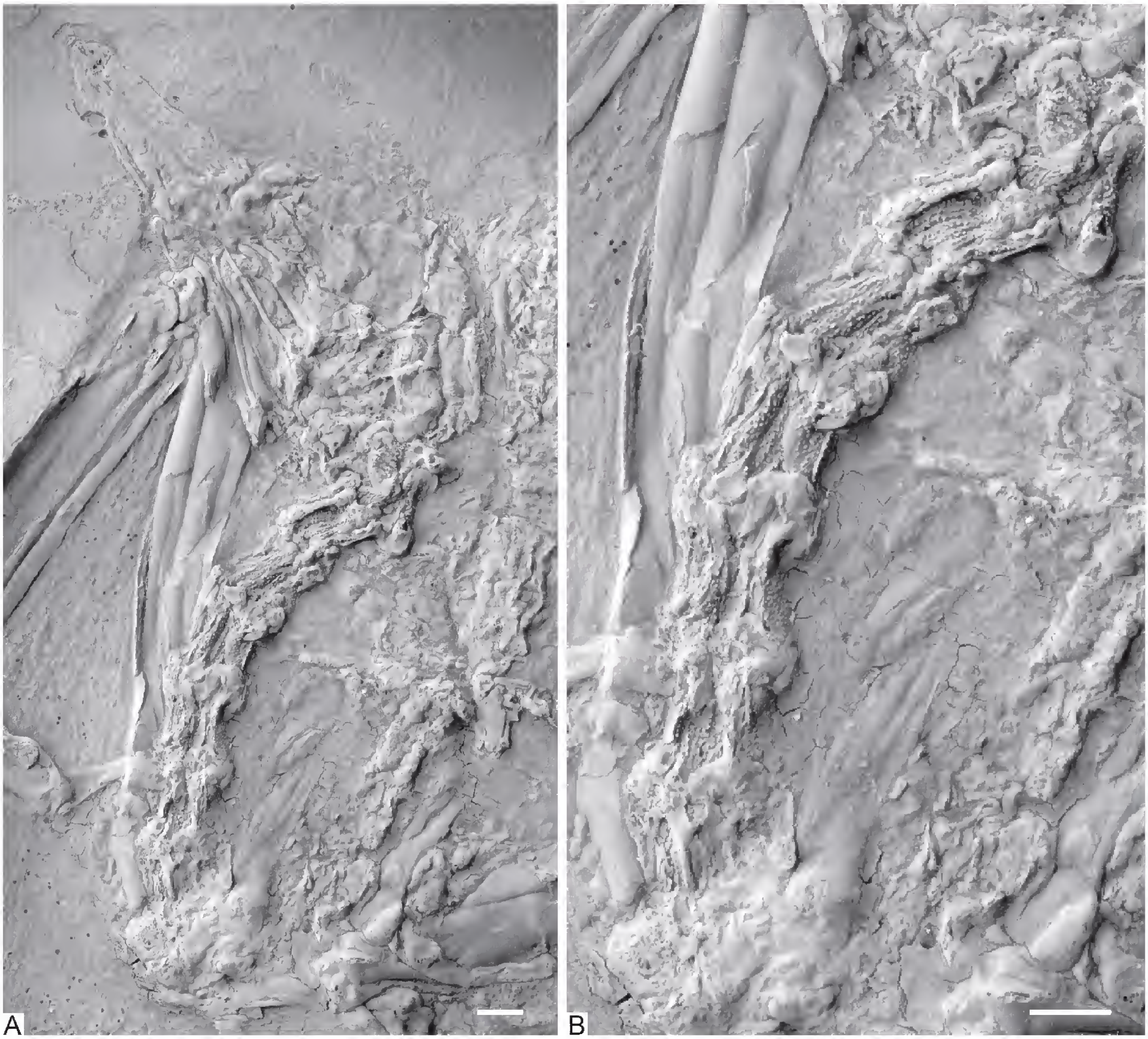

Figure 4. *Perplexicervix microcephalon* n.gen. and n.sp., skull and cervical vertebrae of Pohl specimen (*A*), and detail of cervical vertebrae (*B*). Coated with ammonium chloride to enhance contrast; scale bars equal 5 mm.

very small. In all specimens except HLMD-Me 14996a+b, in which they are not preserved, the cervical vertebrae are densely covered with numerous small tubercles (Fig. 2). The morphology of these tubercles in the referred specimens SMF-ME 10846 and SMF-ME 3548 was described by Mayr (2007), and this description also matches the tubercles in the other specimens. In the privately owned specimen in the Pohl collection it can be seen that the tubercles cover the first nine cervical vertebrae (Fig. 4). The thoracic vertebrae lack tubercles. As in extant Anhimidae, they exhibit a pneumatic foramen on the lateral surface of the corpus (SMF-ME 11211a, SMF-ME 2559a; Fig. 3c).

The robust and broadly rounded processus acrocoracoideus of the right coracoid can be seen in ventral view in HLMD-Me 14996a (Fig. 5a); in its shape it resembles the processus acrocoracoideus of the Otididae. Although only a small portion of the dorsal surface of the extremitas sternalis is visible in HLMD-Me 14996b, distinct muscle striae can be discerned.

The cranial end of the left scapula is exposed in lateral view in HLMD-Me 14996b (Fig. 5b). The acromion is short and there is a well-developed tuberculum coracoideum which indicates the presence of a cup-like cotyla scapularis on the coracoid.

In the holotype only the poorly preserved distal portions of the humeri are visible, and more details of the bone can be discerned in SMF-ME 2559a and HLMD-Me 14996a+b. Being fairly elongate, with a rather narrow proximal and a wide distal end, it resembles the humerus of the Cathartidae in its proportions. There crista deltopectoralis is long but not very prominent, and there seems to have been a convex crista bicipitalis (HLMD-Me 14996a, left side). The small tuberculum dorsale is visible on the left humerus of HLMD-Me 14996b. The distal end only allows the recognition of the ventrally protruding epicondylus ventralis, which bears two marked pits on its ventral surface (HLMD-Me 14996a, SMF-ME 2559a).

The ulna exceeds the other limb bones in length, but only

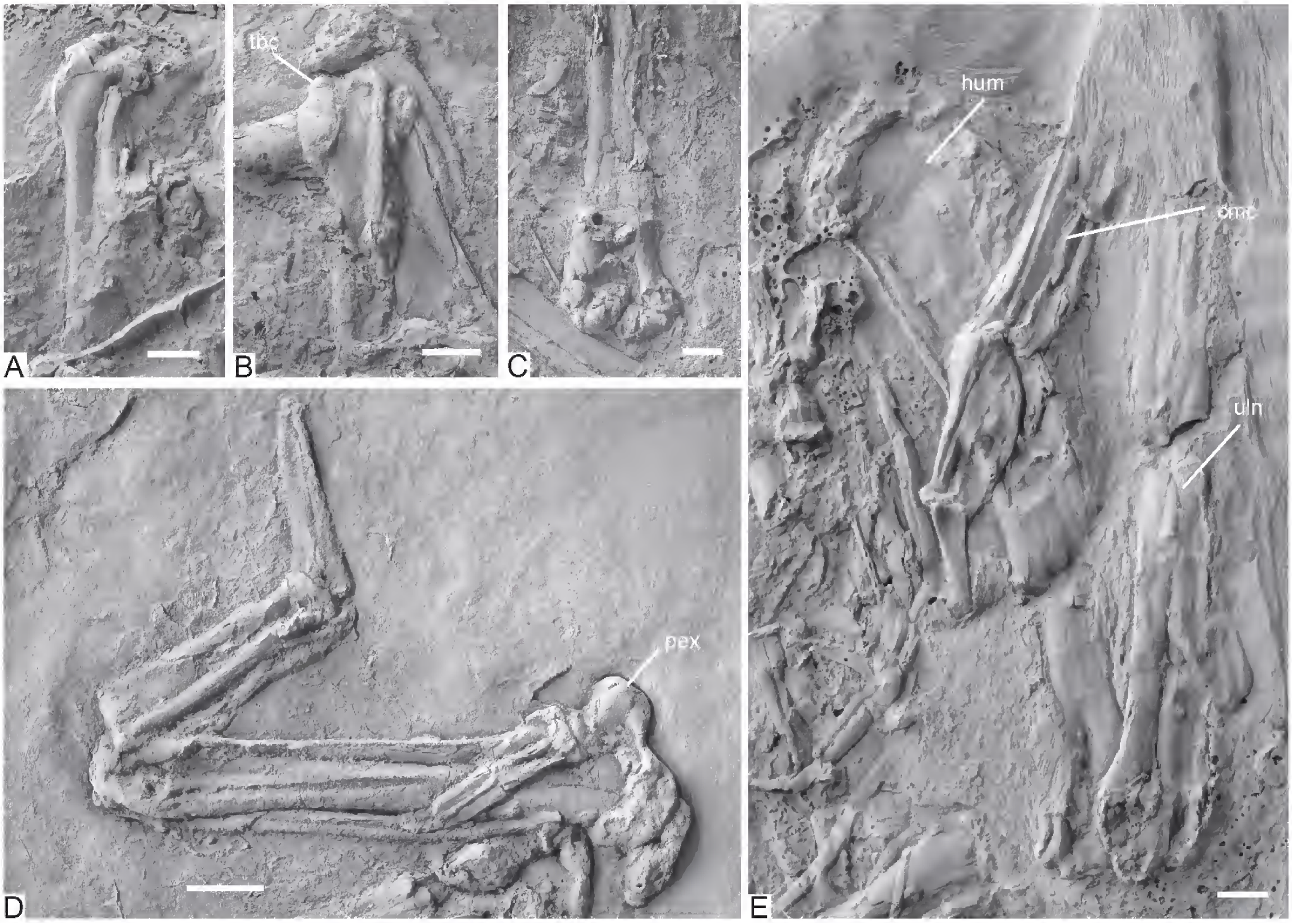

Figure 5. *Perplexicervix microcephalon* n.gen. and n.sp., selected skeletal elements. (*A*) extremitas omalis of right coracoid in ventral view (HLMD-Me 14996a); (*B*) cranial end of left scapula (HLMD-Me 14996b); (*C*) distal end of right humerus in cranial view (HLMD-Me 14996b); (*D*) left manus of holotype (SMF-ME 11211a); (*E*) left wing (HLMD-Me 14996a). Abbreviations: *cmc*—carpometacarpus, *hum*—humerus, *pex*—processus extensorius; *tbc*—tuberculum coracoideum, *uln*—ulna. Coated with ammonium chloride to enhance contrast; scale bars equal 5 mm.

few details of its articular ends can be discerned. The cotyla ventralis seems to have been shallow and the olecranon is short (SMF-ME 11211a, SMF-ME 2559a). In the holotype, the poorly preserved distal end of the left ulna is exposed in ventral view and allows the recognition of a short condylus dorsalis and a small tuberculum carpale. The small condylus dorsalis can also be seen on the right ulna of HLMD-Me 14996a and in SMF-ME 2559a.

The carpometacarpus is slender and fairly long, of similar overall proportions to that of Cathartidae. The prominent processus extensorius has a broadly rounded tip (Fig. 5d) and resembles that of the Turkey Vulture, *Cathartes aura*. The os metacarpale minor is straight, the spatium intermetacarpale narrow, and the symphysis metacarpalis distalis fairly long.

The phalanx digiti alulae is long and lacks an ungual phalanx. The phalanx proximalis digiti majoris exhibits a small processus internus indicis of similar shape to that of *Cathartes aura* (SMF-ME 11211a).

The pelvis of SMF-ME 11211a is visible in ventral view. There are low tubercles on what I consider to be a portion of the left ischium.

The femur of the holotype bears tubercles on the lateral surface of the proximal end and the midsection of the shaft. Although these are somewhat less pronounced than the tubercles on the cervical vertebrae, they are nevertheless very distinct. Such tubercles are absent on the corresponding parts of the fairly well-preserved femora of the referred specimen HLMD-Me 14996a+b.

The tibiotarsus of the holotype is broken in its distal part and the two portions are displaced against each other, thus probably indicating a fracture rather than a breakage due to diagenetic processes. The cristae cnemiales are well developed, and the crista cnemialis cranialis appears to have been proximally protruding (SMF-ME 2559a, right tibiotarsus). The condyles are widely separated and dorsoventrally low, the condylus medialis being smaller than the condylus lateralis; whether an ossified pons supratendineus was present cannot be discerned (SMF-ME 2559a).

The tarsometatarsus of the holotype is broken in its distal fourth and the two parts are dislocated and turned against each other (Fig. 6a); the proximal portion of the bone is visible in plantar view, whereas the dorsal surface of the distal fragment is exposed. In HLMD-Me 14996a+b the left tarsometatarsus is embedded in a dorsoventral position, whereas the right one can be seen in mediolateral view.

The tarsometatarsus of *P. microcephalon* is long and

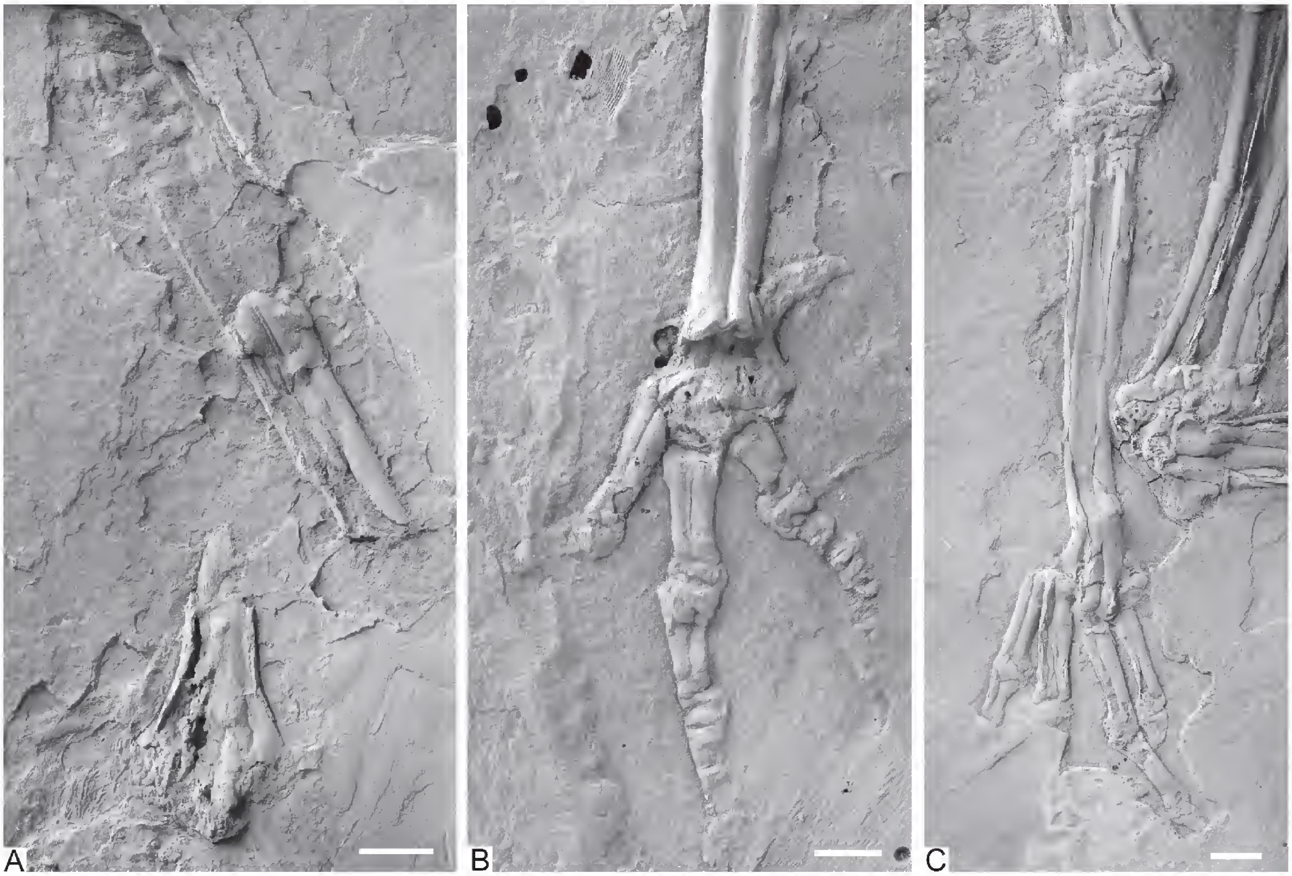

Figure 6. *Perplexicervix microcephalon* n.gen. and n.sp., foot. (*A*) holotype (SMF-ME 11211b), right side; (*B*) HLMD-Me 14996a, left side; (*C*) Pohl specimen, right side. Coated with ammonium chloride to enhance contrast; scale bars equal 5 mm.

slender, the shaft of equal width over most of its length, becoming only slightly narrower distally. The distal end itself is wide and appears to have had a fairly symmetrical shape, with short trochleae metatarsorum II et IV. The hypotarsus is visible through the reverse of the transparent slab of SMF-ME 11211a, but in this specimen it can only be discerned that it bears wide and shallow grooves. The better preserved plantar surface of the left hypotarsus is visible in HLMD-Me 14996b. It has a triangular outline and bears two low ridges, the lateral one of which is larger, and in the medial portion there is a small, nearly closed sulcus. The foramen vasculare distale cannot be discerned in HLMD-Me 14996; in the holotype, there is a large ovate opening in the area of this foramen which does, however, not perforate the bone and seems to be a preparation artifact.

In the holotype only a resin mould of the long hallux is preserved, and in HLMD-Me 14996a+b the toes are badly deformed, which makes it difficult to discern the length of some phalanges (Fig. 6b). However, at least the proximal phalanges of the second and third toes are of average proportions. Next to the lateral side of the left tarsometatarsus of HLMD-Me 14996a, there is a narrow elongate bone, which I interpret as the os metatarsale I.

In SMF-ME 11211a faint shadows of the right wing feathers are visible and, as preserved, the outermost primary measures about 110 mm. Remains of the long wing feathers are also preserved in HLMD-Me 14996a+b, but do not allow a meaningful description.

Discussion

Perplexicervix microcephalon n.gen. and n.sp. measures only about half of the size of *Idiornis tuberculata* (length of tibiotarsus ca. 71 versus 130 mm), and exhibits very different limb proportions. Whereas the ulna is only slightly longer than the cranium in *I. tuberculata* (the beak of this species is unknown), the bone measures nearly 1.5 times the length of the entire skull in *P. microcephalon* (the absolute lengths are 79.5–85 mm in the holotype of *P. microcephalon* versus only 64 mm in the holotype of the much larger *I. tuberculata*). *Perplexicervix microcephalon* is further distinguished from *Idiornis* in the morphology of the carpometacarpus (proportionally much shorter and with a bowed os metacarpale minus in *Idiornis*) and coracoid (in *Idiornis* the processus acrocoracoideus is connected by an osseous bridge with the processus procoracoideus), as well as the proportionally shorter tarsometatarsus.

The presence of a tuba auditiva communis and a bicondylar processus oticus of the quadrate support a position of *P. microcephalon* within neognathous birds (e.g., Cracraft, 1988). Within extant Neognathae, functional processus basipterygoidei occur in galloanserine birds, some Procellariiformes and Charadriiformes, Columbiformes, Cathartidae, Sagittariidae, Strigiformes, Trogonidae, and some taxa of the Strisores sensu Mayr (2010), i.e., the clade including nightjars, swifts, hummingbirds, and allies. Of these taxa, *P. microcephalon* most closely resembles the anseriform Anhimidae and the Cathartidae in overall morphology, but the incomplete knowledge of its osteology does not allow an reliable phylogenetic assignment of the peculiar fossil species. Occurrence of processus basipterygoidei and pneumatic openings on the bodies of the thoracic vertebrae in particular indicates affinities to the Anhimidae, and there remains a possibility that *P. microcephalon* is related to as yet undescribed putative early Eocene Anhimidae (Mayr, 2009).

Specimen SMF-ME 3548 is notably larger than the holotype, but the small number of known specimens does not allow an unambiguous assessment whether this indicates specific difference or sexual dimorphism in size. The long wings indicate that *P. microcephalon* was capable of sustained flight. Judging from the relatively wide and short beak, which only has a very slightly hooked tip, *P. microcephalon* may have fed on either plant matter or soft-bodied invertebrates.

The origin and significance of the vertebral tubercles remains mysterious. Their presence in two avian species without close relationship is in agreement with earlier assumptions, that these unusual structures are of pathologic origin (Mayr, 2007; see also Peters, 1995). This hypothesis gets further support from the fact that small tubercles are present on the femur of the holotype, but absent on the femora of HLMD-Me 14996a+b. As I have detailed previously (Mayr, 2007), the regular structure and symmetric distribution of the tubercles may indicate a systemic, i.e., metabolic or endocrine, disorder. If they were caused by, for example, high doses of phytohormones or an extinct group of pathogens, there may well have been an accumulation within taxonomically restricted avian groups with a similar feeding ecology or habitat. However, in conflict with a pathologic origin is the fact that these tubercles occur in all specimens of *P. microcephalon* with preserved cervical vertebrae, i.e. in no less than five of the six known specimens. If the tubercles represent a true morphological feature, it is difficult to imagine what function they may have fulfilled, and why similar structures are unknown from extant birds.

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New Birds from the Lower Eocene Green River Formation, North America

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ABSTRACT. The Lower Eocene Green River Formation has yielded a large number of hitherto mostly undescribed birds. In this study, I describe a new species and genus as the first representative of Zygodactylidae from the New World. Furthermore, new specimens are referred to *Gallinuloides wyomingensis* (Galliformes), *Messelornis nearctica* (Gruiformes), and *"Neanis" kistneri* (?Galbulae). Based on the new specimens, I reveal additional information on the osteology and the systematic affinities of these species. The new specimens corroborate the fact that there is a strong similarity between the Green River avifauna and that of the roughly contemporaneous avifauna of Messel (Germany). In both sites, Messelornithidae and small arboreal birds are predominant in the fossil record.

WEIDIG, ILKA, 2010. New birds from the Lower Eocene Green River Formation, North America. In *Proceedings of the VII International Meeting of the Society of Avian Paleontology and Evolution*, ed. W.E. Boles and T.H. Worthy. *Records of the Australian Museum* 62(1): 29–44.

Situated in Wyoming, Utah and Colorado (USA), the Green River Formation was formed in the early Tertiary when the climate was warm-temperate to subtropical (Grande 1980). The Green River Formation contains the largest number of complete or nearly complete articulated bird skeletons from the North American Tertiary (Grande, 1980). However, only few species are described so far, and most of these species are based on a single specimen each. The first fossil bird described from the Green River Formation was the galliform *Gallinuloides wyomingensis* Eastman, 1900. Among the more abundant taxa from the Green River Formation are the Presbyornithidae with *Presbyornis pervetus* Wetmore, 1926, which were described in detail by Feduccia & McGrew (1975) as well as Olson & Feduccia (1980) and Ericson (1997, 1999, 2000). Additional taxa include gruiform, "caprimulgiform" and coraciiform birds (for details see Table 1).

In this paper, a new species referred to Zygodactylidae Brodkorb, 1971, which so far were only known from the Old World, as well as new specimens of three already known Green River species, *Gallinuloides wyomingensis* Eastman, 1900, *Messelornis nearctica* Hesse, 1992, and *Neanis kistneri* (Feduccia, 1973), are described.

Material and methods

Osteological nomenclature follows Baumel & Witmer (1993). The dimensions are in millimetres and they represent the overall length of the bone along its longitudinal axis. The following abbreviations are used to indicate the collections in which the specimens are deposited: BHI Black Hills Institute, Black Hills, South Dakota, USA; FMNH Field Museum of Natural History, Chicago, Illinois, USA; MCZ Museum of comparative Zoology, Cambridge, Massachusetts, USA, NAMAL North American Museum of Ancient Life, Lehi, Utah, USA; SMF Senckenbergmuseum Frankfurt, Germany; SMNK Staatliches Museum fuer Naturkunde Karlsruhe, Germany; USNM National Museum of Natural History, Washington, DC, USA; UWGM University of Wyoming Geological Museum, Laramie, Wyoming, USA; WDC Wyoming Dinosaur Center, Thermopolis, Wyoming, USA.

Table 1. Hitherto described bird taxa from the Green River Formation.

taxon			references
Lithornithiformes	Lithornithidae	*Pseudocrypturus cercanaxius* Houde, 1988	Houde (1988)
Pelecaniformes	Limnofregatidae	*Limnofregata azygosternon* Olson, 1977	Olson (1977)
Pelecaniformes	Limnofregatidae	*Limnofregata hasegawyi* Olson & Matsuoka, 2005	Olson & Matsuoka (2005)
?Phoenicopteriformes	Juncitarsinae	*Juncitarsus merkeli* Peters, 1987	Peters (1987)
Anseriformes	Presbyornithidae	*Presbyornis pervetus* Wetmore, 1926	Feduccia & McGrew (1975), Olson & Feduccia (1980), Ericson (1997, 1999, 2000)
Galliformes	Gallinuloididae	*Gallinuloides wyomingensis* Eastman, 1900	Eastman (1900), Mayr & Weidig (2004), this study
Gruiformes	Messelornithidae	*Messelornis nearctica* Hesse, 1992	Hesse (1992), this study
ordo inc. sed.	Foratidae	*Foro panarium* Olson, 1992	Olson (1992)
"Caprimulgiformes"	Preficinae	*Prefica nivea* Olson, 1987	Olson (1987)
"Caprimulgiformes"	Fluvioviridavidae	*Fluvioviridavis platyrhamphus* Mayr & Daniels, 2001	Mayr & Daniels (2001)
Coraciiformes s.s.	Primobucconidae	*Primobucco mcgrewi* Brodkorb, 1970	Brodkorb (1970), Mayr *et al.* (2004)
ordo inc. sed.	?Leptosomidae	*Plesiocathartes wyomingensis* Weidig, 2006	Weidig (2006)
ordo inc. sed.	?Leptosomidae	*Plesiocathartes major* Weidig, 2006	Weidig (2006)
?Piciformes	?Gracilitarsidae	*Neanis schucherti* Shufeldt, 1913	Shufeldt (1913)
?Piciformes	?Galbulae	*"Neanis" kistneri* Feduccia, 1973	Feduccia (1973), this study
Psittaciformes	Messelasturidae	*Tynskya eocaena* Mayr, 2000	Mayr (2000b)
Psittaciformes	Halcyornithidae	*"Primobucco" olsoni* Feduccia & Martin, 1976	Feduccia & Martin (1976)
Coliiformes	Sandcoleidae	*Anneavis annae* Houde & Olson, 1992	Houde & Olson (1992)
Passeriformes	Zygodactylidae	2 species	this study

Systematics

Galliformes Temminck, 1820

Gallinuloididae Lucas, 1900

Included genera: *Gallinuloides* Eastman, 1900, *Paraortygoides* Mayr, 2000.

Gallinuloides wyomingensis Eastman, 1900

Holotype. MCZ 342221, complete articulated skeleton on a slab.

Referred specimen. WDC-CGR-012, complete articulated skeleton, from the 18-inch-layer (F1-locality of Grande, 1980), Upper Fossil Butte Member of Fossil Lake, Kemmerer, Wyoming (Fig. 1) (also shown in Mayr & Weidig, 2004).

The locality of the holotype (MCZ 342221) is described as "fish-bearing shales near Fossil, Wyoming" by Eastman (1900: 54), which, according to Grande (1980), belongs to the same locality as the WDC specimen.

Remarks. An emended diagnosis of the Gallinuloididae, a differential diagnosis to separate *Gallinuloides* from *Paraortygoides*, characters pertinent to the systematic position of Gallinuloididae as well as the dimensions of the WDC specimen are already given in Mayr & Weidig (2004). In the following, additional characters of *Gallinuloides wyomingensis* visible on the WDC specimen are described.

Description. The skull of *Gallinuloides* is small in relation to overall body size as in other galliform birds. The beak of this fossil bird is relatively short and its oval nasal openings are large. *Gallinuloides* differs from extant galliforms in having a small processus postorbitalis, lacking an ossified aponeurosis zygomatica, having a well-developed os ectethmoidale (Mayr & Weidig, 2004) and a rather small prefrontal. In accordance with modern galliforms, the foramen magnum is shifted caudad. On the quadratum, the small knob between the processus oticus and the processus mandibularis which occurs in all Cracidae is absent in *Gallinuloides*.

The mandible of *Gallinuloides* has a short symphysis mandibularis and fenestrae mandibulares seem to be absent. Lucas (1900) stated that a processus retroarticularis is not present; in this respect, *Gallinuloides* would differ from all modern galliforms. However, the mandible of the holotype is only very poorly preserved and the presence, or absence, of a processus retroarticularis cannot be determined. Unfortunately, the WDC-CGR-012 specimen cannot clarify this point. Due to a slight slant of the mandible, the caudal end is not clearly visible and it is not possible to discern whether a processus retroarticularis is present.

The coracoid is rather stout; the processus acrocoracoideus is somewhat larger than that of *Paraortygoides* and is slightly hooked. In agreement with *Paraortygoides* and *Paraortyx* (Mayr, 2000a; Mourer-Chauviré, 1992), a very small processus procoracoideus is present. The processus lateralis of the coracoid is only moderately extended, but, in contrast to extant genera, is divided into two tips. The facies articularis sterni is very high as in modern galliforms.

The humerus most closely resembles that of the extant *Leipoa ocellata* (Megapodiidae) and has a rounded and short crista deltopectoralis. Eastman (1900) remarked that *Gallinuloides* has a "broad deltopectoral crest"; however, it is not very broad for a galliform bird, having approximately the same relative size as that of *Leipoa* and is thus somewhat larger than that of *Paraortygoides*. As in extant galliforms, the ventral surface of the crista deltopectoralis is perpendicular to the cranial surface of the humerus shaft. The crista bicipitalis is rather small and the humeral shaft is slightly sigmoidally curved. The fossa m. brachialis is large but only moderately deep as in modern *Leipoa, Alectura* (Megapodiidae) and *Ortalis* (Cracidae). The tuberculum supracondylare ventrale is rather pronounced.

The ulna is considerably curved and shows no papillae remigiales, its overall morphology resembles that of *Paraortygoides*. However, in contrast to *Paraortygoides*, the ulna of *Gallinuloides* is slightly longer than the humerus. The olecranon of *Gallinuloides* is moderately long, it is slightly

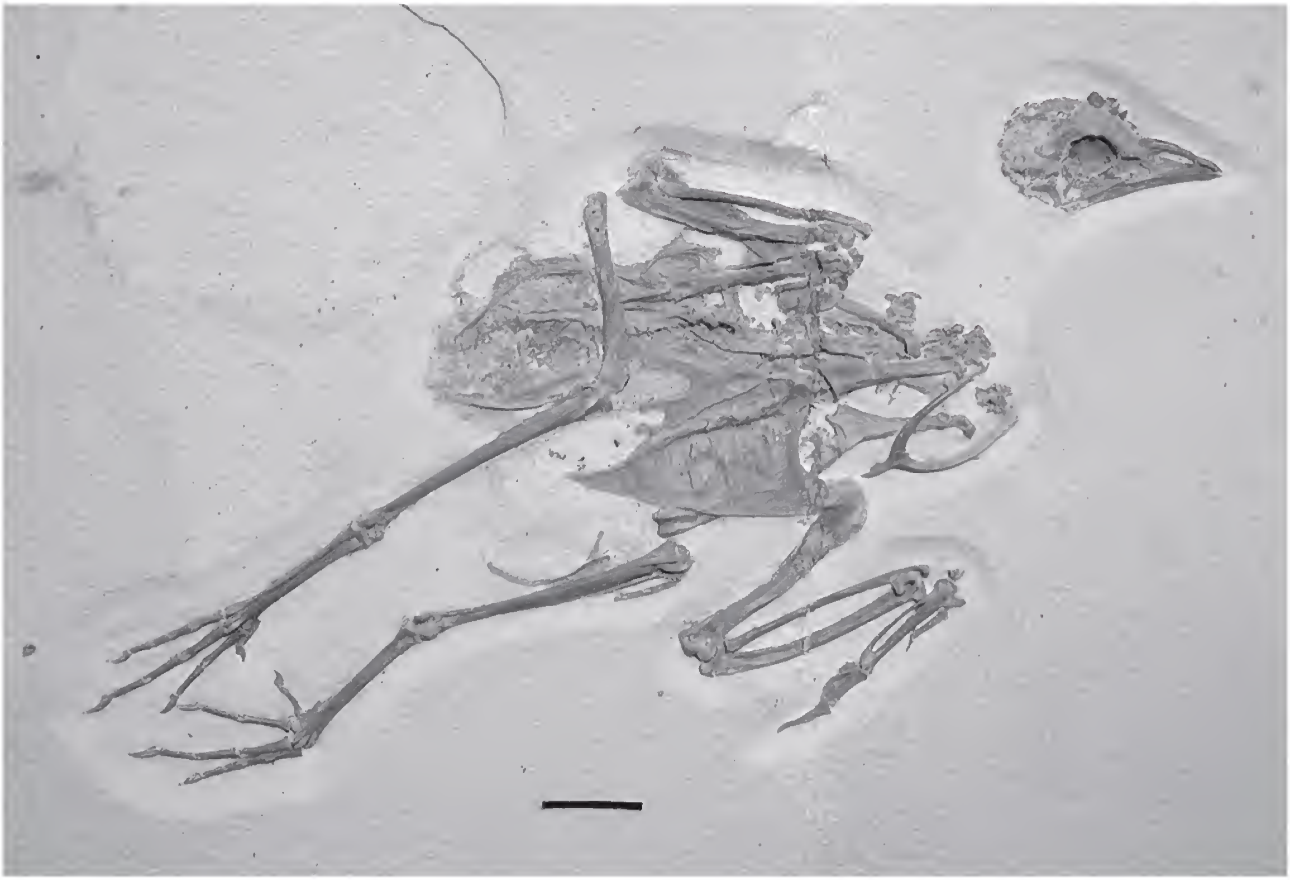

Figure 1. *Gallinuloides wyomingensis*, referred specimen WDC-CGR-012, scale bar 20 mm.

longer than that of *Paraortygoides*. An impressio brachialis is present. The dorsal side of proximal end bears a distinct impression, distally of the processus cotylaris dorsalis. This impression is also exhibited by *Paraortygoides* (Mayr, 2000a) and the cracids.

The carpometacarpus resembles that of *Paraortygoides*, the ossa metacarpalia are straight and parallel, the spatium intermetacarpale is narrow (Mayr & Weidig, 2004). The processus extensorius is large, and its tip is pointed proximo-cranially. The distal end of the carpometacarpus resembles that of *Paraortygoides* very closely: the synostosis metacarpalis distalis is long and fairly wide, the os metacarpale majus protrudes cranially, and the proximal phalanx of the digitus major has a long, deep sulcus and a deep, but small, oval fenestration. The distal phalanx of the digitus majoris distalis is longer than the proximal phalanx and the digitus alulae bears a claw.

In accordance with the condition seen in extant galliforms and *Paraortygoides*, the tibiotarsus of *Gallinuloides* is the longest limb element. The proximal end bears medium-sized cristae cnemiales. At the distal end, the condylus medialis is narrower mediolaterally than the condylus lateralis but protrudes considerably farther cranially. The same proportions are found in modern galliforms. However, in contrast thereto, both condyli have about the same size in *Paraortygoides* (Mayr, 2000a). The incisura intercondylaris is narrower than in *Paraortygoides*. A comparatively broad pons supratendineus is present.

The tarsometatarsus measures about two thirds of the length of the tibiotarsus. Not many details are discernible on the proximal end of the tarsometatarsus. At least one foramen vasculare proximale is present. The hypotarsus is not visible in either the holotype or the new specimen, therefore Lucas' (1900) comments on it are only speculation. The tarsometatarsus of *Gallinuloides* has a large foramen vasculare distale, that of *Paraortygoides* is smaller. In distal view, the trochleae metatarsorum are situated along a curved line. The trochlea metatarsi III is the longest trochlea, followed by the trochlea metatarsi IV. The trochlea metatarsi II is considerably shorter than the trochlea metatarsi IV. In *Gallinuloides*, the trochlea metatarsi II extends plantad, to approximately the same degree as in *Paraortygoides*.

Discussion. Since the original description of *Gallinuloides wyomingensis*, various taxa have been included in the Gallinuloididae, and different systematic positions have been proposed (see e.g., Crowe *et al.*, 2006; Crowe & Short, 1992; Dyke, 2003; Lucas, 1900; Mayr, 2008a; Mayr & Weidig, 2004). Based on the WDC specimen, Mayr & Weidig (2004) published an amended diagnosis of the Gallinuloididae, including only *Gallinuloides* and *Paraortygoides* in the taxon. According to Mayr & Weidig (2004), the Gallinuloididae belong to the stem-group of the Galliformes and represent a sister-taxon to all modern crown-group galliforms, since they exhibit several plesiomorphic characters such as the presence of a well-developed os ecthemoidale, poorly developed processus postorbitales, a cup-like cotyla scapularis of the coracoid, a long, slender scapula with a pointed caudal end, robust scapi claviculae of the furcula, a sternum with an apex carinae that is not displaced caudally, a narrow, elongated carpometacarpus with a straight os metacarpale minus, splayed trochleae metatarsorum, and the absence

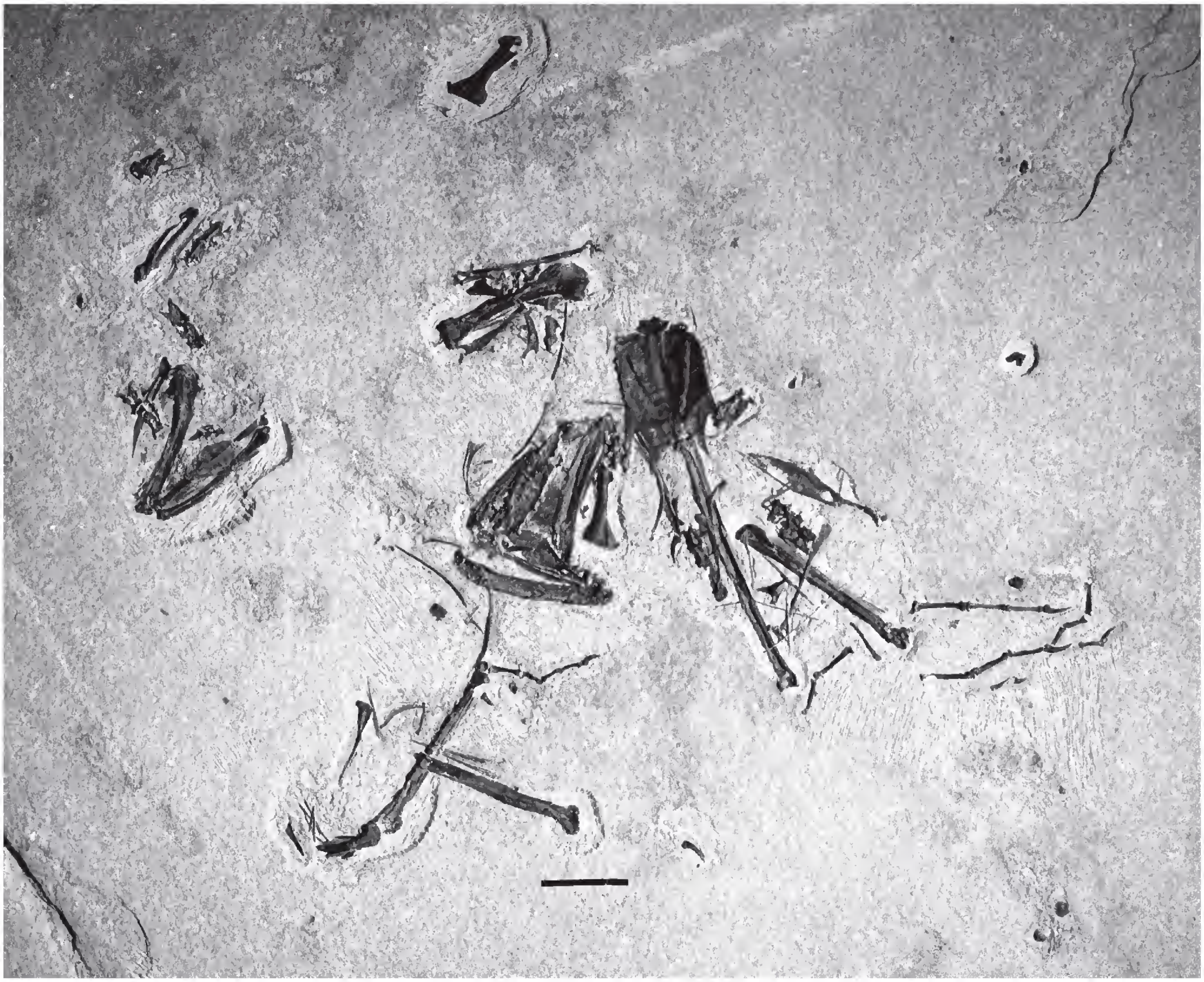

Figure 2. *Messelornis nearctica*, FMNH A 716, scale bar 20 mm.

of ossified tendons. This result was recently supported by a phylogenetic revision using both morphological and molecular data of *Gallinuloides wyomingensis* and modern galliforms undertaken by Ksepka (2009), which also placed *Gallinuloides* clearly outside crown-group galliforms.

Messelornithidae Hesse, 1988

Included genera: *Messelornis* Hesse, 1988, *Itardiornis* Mourer-Chauviré, 1995.

Messelornis nearctica Hesse, 1992

Holotype. SMF Av 406, complete skeleton.

Referred specimens. FMNH A 716, disarticulated partial skeleton lacking the skull and distal ends of the wings (Fig. 2); SMNK-PAL 3810, nearly complete skeleton with feather remains (Fig. 3); USNM 776273, partial skeleton lacking the skull and the left wing (Fig. 4); USNM 336269, right leg with foot, parts of the pelvis and some vertebrae (Fig. 5); USNM 336277, left leg with foot, slab and counterslab (Fig. 6); BHI 1283, left leg, pelvis (Fig. 7); BHI 1292, both legs, pelvis, some vertebrae; BHI 1294, parts of the sternum, wing (Fig. 8); tentatively referred: USNM 776275, tip of bill, crushed skull, both wings, coracoid.

The new specimens exhibit the typical features of Messelornithidae (Hesse, 1992) such as skull with nostrils extending far forward, compact, bowed ulna with short, broad, blunt olecranon, carpometacarpus with broad processus extensorius, tarsometatarsus with short, broad trochlea metatarsi III. Contrary to Hesse's (1992) diagnosis, the trochlea metatarsi IV is longer than trochlea metatarsi II. According to Hesse (1992), *M. nearctica* differs from other members of the family mainly in details of the hypotarsus which are not recognizable in any of the new specimens. Additionally, the toes are longer and more slender compared to *M. cristata* (Hesse, 1992), a character which can also be seen in the new specimens. In addition to the features mentioned by Hesse, the os metacarpale minus is slightly longer than the os metacarpale majus in *M. nearctica* (same length in *M. cristata*).

Dimensions. see Table 2 and 3.

Description. The new specimens differ considerably in size (Table 1). This is in accordance with the type species of Messelornithidae, *Messelornis cristata* from Messel (Hesse, 1988a; Hesse & Habersetzer, 1993). A detailed description of the holotype of *M. nearctica* is given by Hesse (1992). In the following, only new features visible on the referred specimens are mentioned.

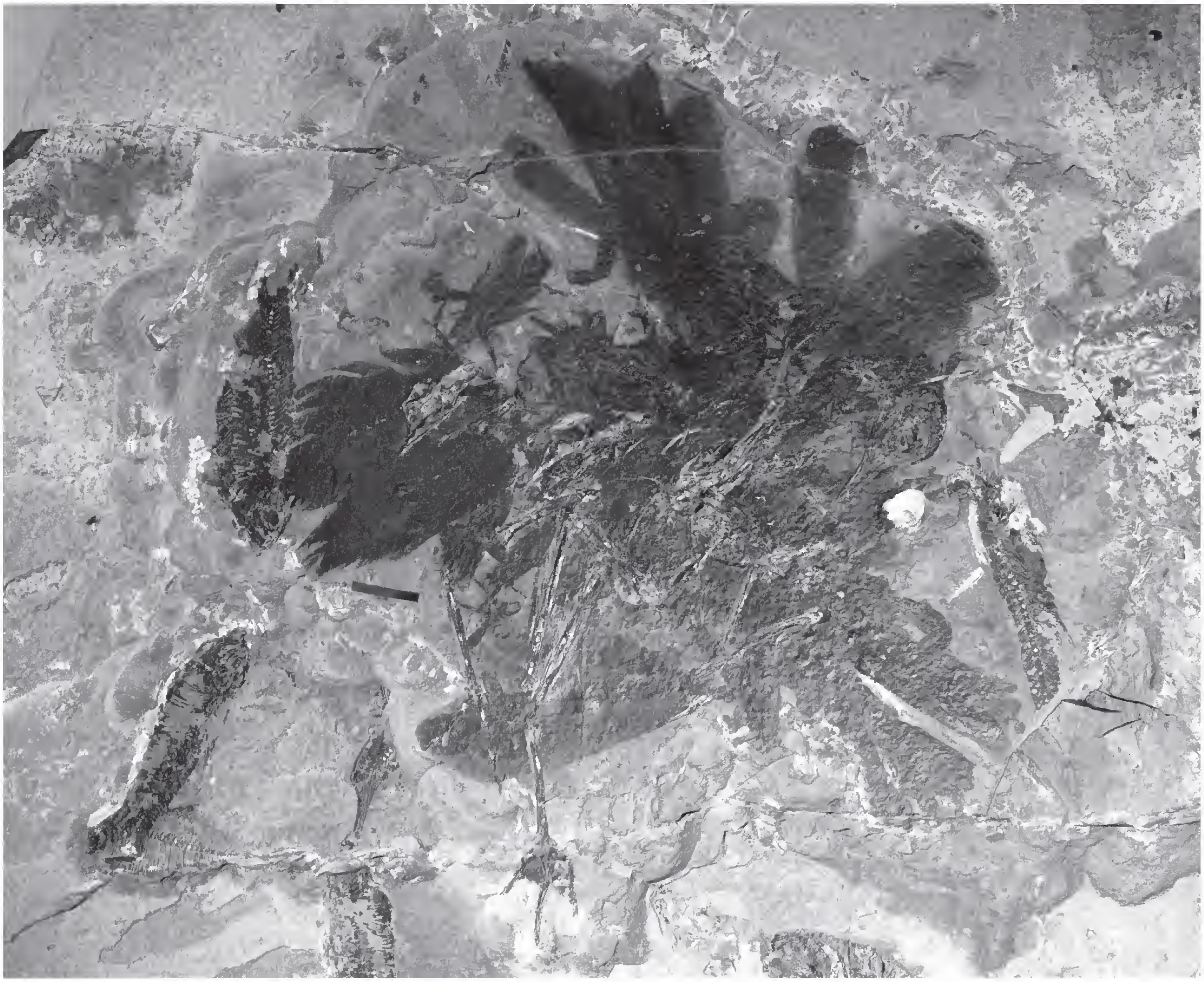

Figure 3. *Messelornis nearctica*, SMNK-PAL 3810, scale bar 20 mm.

The coracoid is short, but not as broad as in *Itardiornis*. The processus acrocoracoideus is hooked. The processus procoracoideus is very large as in *Eurypyga*. On the cranial surface two marked lines are visible. The angulus medialis is blunt and broad. A short but pronounced facies is visible dorsally of the facies articularis sternalis. The U-shaped furcula is small and rather wide; it seems to have a very small apophysis furculae. The scapula is short, but slender. It broadens in the curvature, the caudal end is pointed.

The sternum is moderately long and rather slender. A spina externa is not visible. Four incisurae intercostalis are present. The margo costalis reaches far caudad, it is nearly half as long as the whole sternum. The margo caudalis is not completely preserved in any of the specimens. Hesse (1992) stated that the taxon Eurypygoidea (Eurypygidae + Messelornithidae) is characterized by a "short, broad sternum, with two to three notches on each side" (Hesse 1992:171). The new specimens show at least two incisurae, i.e. one per side. Since the middle portion of the margo caudalis is not preserved in any specimen, it is not possible to determine the exact number of incisurae. In relation to the total sternum length, the incisurae are deeper than in *Eurypyga*.

The humerus resembles that of *Messelornis cristata*. The tuberculum supracondylare ventrale is extremely pronounced and sharp. The humerus shaft is bowed. The condylus ventralis is proximo-distally narrow, and sharp. As in *Itardiornis*, the sulcus transversus is short, but well marked. The ulna is already described in detail in Hesse (1992). Hesse (1992: 173) stated that the "humerus (is) a little shorter than ulna". This is not true for the new specimens, both in the FMNH PA 716 and the SMNK PAL 3810 specimen the ulna is shorter than the humerus (Table 2). The os metacarpale minus of the carpometacarpus is straight; a very small processus intermetacarpalis is present as in *Messelornis cristata* and *Itardiornis*. In contrast to *Messelornis cristata*, the os metacarpale minus seems to be slightly longer than the os metacarpale majus. Hesse (1992) stated that the carpometacarpus is shorter in relation to the wing than in *Messelornis cristata*. However, the difference in length between the holotype of *Messelornis nearctica* and of *Messelornis cristata* is only very small (21% in *Messelornis nearctica* versus 22.4% in *Messelornis cristata*, Hesse, 1988a). The new specimens show that this character is somewhat variable, they differ in their relative length of the carpometacarpus (up to 23.2% in the FMNH PA 716 specimen), which is not shorter than in *Messelornis cristata*.

The pelvis has a long processus terminalis ischii, which reaches the pubis. The foramen obturatum seems to be closed. The femur is strongly bowed. A trochlea fibularis is present with a high lateral edge. The tibiotarsus is the longest

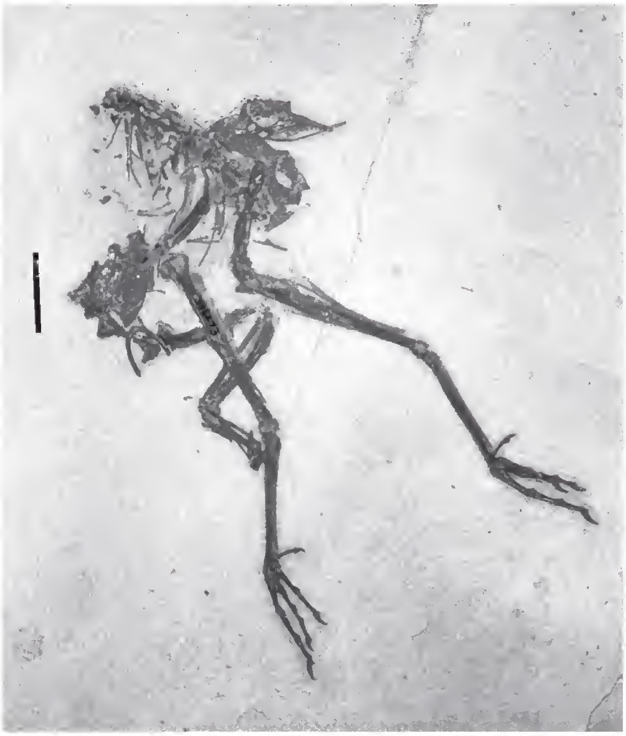

Figure 4. *Messelornis nearctica*, USNM 776273, scale bar 20 mm.

limb element. The proximal end of the tibiotarsus shows large cristae cnemiales; the crista fibularis is pronounced. A sulcus m. fibularis is not visible in any specimen, probably due to poor preservation. The trochlea cartilaginis tibialis is proximo-distally low, but caudo-cranially deep. The tarsometatarsus closely resembles that of *Messelornis cristata*. The hypotarsus is quite small, the number of cristae hypotarsi is not recognizable. The trochlea metatarsi III is the longest, followed by the trochlea metatarsi IV and then the trochlea metatarsi II; the difference in length between trochlea metatarsi IV and trochlea metatarsi II is less distinct than in *Itardiornis*. The trochlea metatarsi II is projected well plantad. The plantar surface of the trochlea metatarsi II is not flattened, but rounded as in *Itardiornis* (Mourer-Chauviré, 1995). A foramen vasculare distale is present. The toes have the usual number of phalanges. Compared to *Messelornis cristata*, the toes are relatively longer.

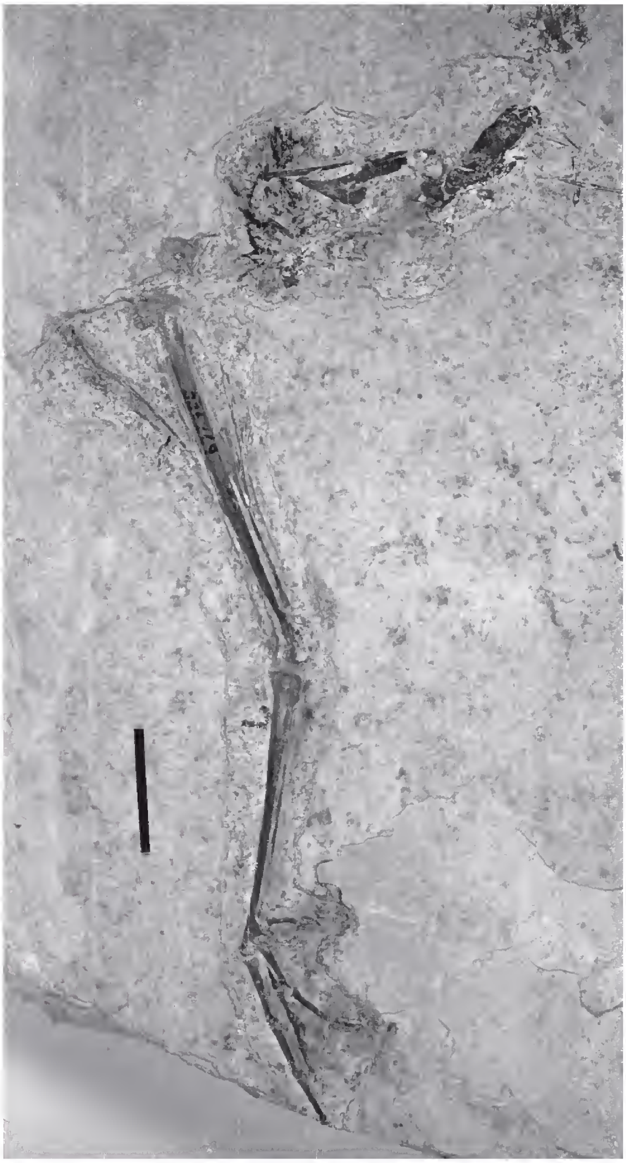

Figure 5. *Messelornis nearctica*, USNM 336269, scale bar 20 mm.

Table 2. *Messelornis nearctica*, length of the limb bones compared to other messelornithids, in mm, measurements of *M. cristata* after Hesse (1988a), measurements of *M. russelli* and *Itardiornis hessae* after Mourer-Chauviré (1995).

	CO	HU	UL	CM	FE	TT	TM
Messelornis nearctica							
SMF Av 406	19.0	35.5	36.0	19.0	35.0	63.0	46.0
FMNH PA 716	20.7	35.9	33.7	20.8	ca. 38.2	63.2	47.4
SMNK PAL 3810	18.2	33.0	32.0	18.5	34.0	52.8	39.2
USNM 336269	—	—	—	—	—	65.0	46.6
USNM 336273	ca. 17.5	ca. 30.0	29.4	16.9	ca. 29.5	50.2	35.1
USNM 336275	18.5	ca. 26.0	33.8	ca. 16.0	—	—	—
USNM 336277	—	—	—	—	ca. 38.7	67.2	48.0
BHI 1283	—	—	—	—	33.7	54.9	—
BHI 1292	—	—	—	—	36.2	64.5	47.3
BHI 1294	—	—	ca. 34.0	17.9	—	—	—
Messelornis cristata							
SMF ME 807a,b,c	21.0	36.0	34.5	20.5	35.0	ca. 62.0	52.5
Messelornis russelli							
BR 14033	—	ca. 52.0	—	—	—	—	—
Itardiornis hessae	31.7	ca. 46.0	—	—	—	—	—

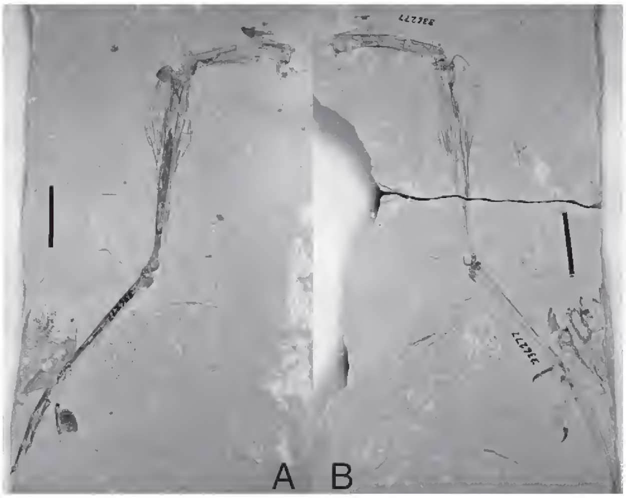

Figure 6. *Messelornis nearctica*, USNM 336277, A = slab, B = counterslab, scale bar 20 mm.

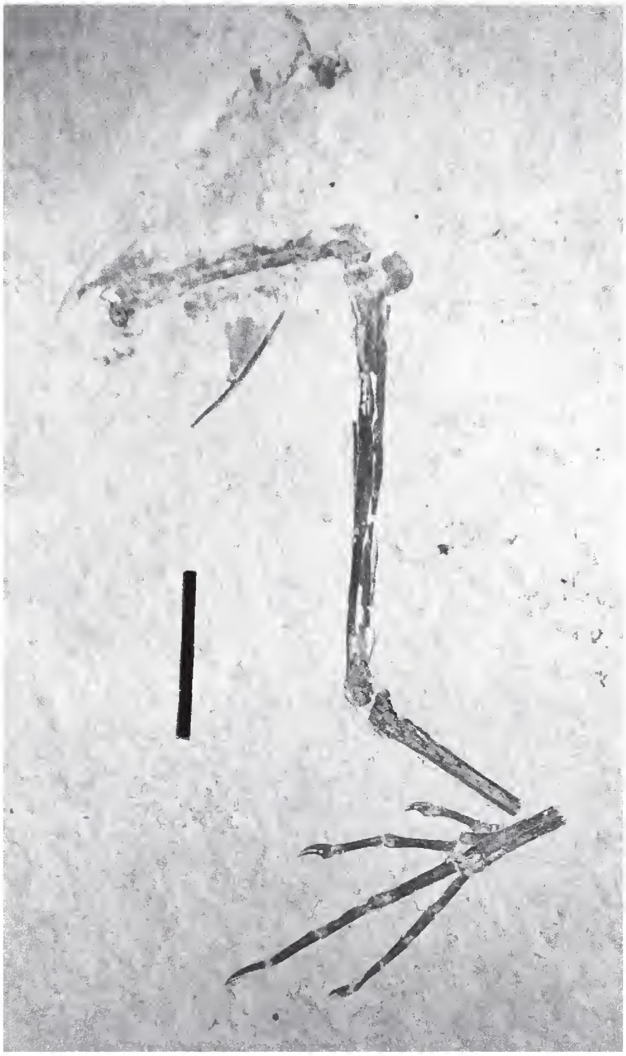

Figure 7. *Messelornis nearctica*, BHI 1283, scale bar 20 mm.

Only in the SMNK PAL 3810 specimen are several scattered feathers preserved. In all specimens, several ossified tendons are preserved. Most occur at tarsometatarsus, tibiotarsus, humerus, radius and ulna. Some tendons are scattered on the slabs, their origin is not discernible. The tendons at the tibiotarsus are split proximally.

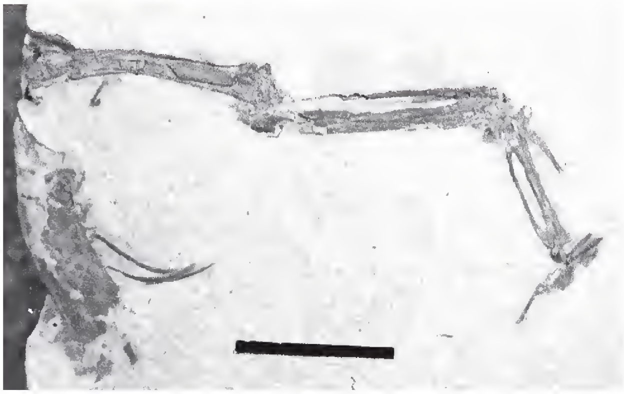

Figure 8. *Messelornis nearctica*, BHI 1294, scale bar 20 mm.

Discussion. The fossil Messelornithidae were originally described by Hesse (1988a). Besides the type species *Messelornis cristata* from Messel, the Messelornithidae comprise *Messelornis russelli* and *Itardiornis hessae* from the Quercy in France (Mourer-Chauviré, 1995), as well as *Messelornis nearctica* from the Green River Formation (Hesse, 1992). Hesse (1988b) regarded the Eurypygidae to be the closest modern relative of the fossil Messelornithidae. This view was widely accepted (e.g., Cracraft, 2001; Peters, 1991) and supported by Livezey (1998) although Mourer-Chauviré (1995) noted some parallelism with Rallidae. Mayr (2004a) regarded the Messelornithidae as the sister-taxon to rails and finfoots and supported his classification with derived characters shared by the taxon (Messelornithidae + (Rallidae + Heliornithidae)).

The type species of the Messelornithidae, *Messelornis cristata*, was thoroughly described (Hesse, 1988a,b, 1990); an extensive study of the osteology of this species was based on a total of 346 specimens. The description of the Green River species *Messelornis nearctica*, however, was based on a single, nearly complete, but crushed specimen (Hesse, 1992). The new specimens described above reveal additional osteological features which have been unknown so far. In addition, they show that some details of the original description (Hesse, 1992) are not wholly correct, because they were only based on one specimen; this mainly concerns size-related features.

Messelornis nearctica has as large a size-range as *Messelornis cristata*. Sexual dimorphism might be an explanation for the large size-range; it is possible to divide the ten specimens described above into two groups: four small specimens (SMNK PAL 3810, USNM 336273, USNM 336275 and BHI 1294) and the remaining six large specimens (Table 2). Hesse (1990) reported that, within the Gruiformes, males tend to have slightly longer limb bones than females, but the length of the limb bones of both sexes overlap considerably. Thus, the Green River specimens might represent four female individuals and six male individuals. However, in *Messelornis cristata*, which is known from a far larger sample, it is not possible to clearly distinguish two groups that represent the sexes (Hesse, 1990).

All Green River specimens seem to be adults, which is in accordance with the findings from Messel (Hesse, 1990). As it was already proposed for *Messelornis cristata* (Hesse, 1990), this might indicate that the nests of *Messelornis nearctica* were not situated directly at the shore of the lake. The adult birds, however, probably spent a considerable

Table 3. *Messelornis nearctica*, proportions of limb bones, compared to the holotype of *Messelornis cristata* (measurements of *Messelornis cristata* after Hesse, 1988a, measurements of *Messelornis russelli* and *Itardiornis hessae* after Mourer-Chauviré, 1995).

	HU:UL	HU:CM	HU:TM	UL:TT	UL:TM	CM:TM	TT:TM
Messelornis nearctica							
SMF Av 406	0.99	1.87	0.77	0.57	0.78	0.41	1.37
FMNH PA 716	1.07	1.73	0.76	0.53	0.71	0.44	1.33
SMNK PAL 3810	1.03	1.78	0.84	0.63	0.82	0.47	1.35
USNM 336273	1.02	1.78	0.85	0.59	0.84	0.48	1.43
Messelornis cristata							
SMF ME 807a,b,c	1.04	1.76	0.69	0.56	0.66	0.39	1.18

amount of time close to the shore, considering the number of adult specimens.

Zygodactylidae Brodkorb, 1971

Included genera: *Zygodactylus* Ballmann, 1969, *Primoscens* Harrison & Walker, 1977, *Primozygodactylus* Mayr, 1998, *Eozygodactylus* n.gen.

Taxonomic remarks. The Primoscenidae Harrison & Walker, 1977 were described based on a single carpometacarpus. Mayr (1998) included additional species which were represented by complete skeletons and emended the diagnosis, mentioning the resemblance of Primoscenidae to the Zygodactylidae Brodkorb, 1971. Due to a new species of Zygodactylidae, Mayr (2008b) synonymized the Primoscenidae Harrison & Walker, 1977 with the Zygodactylidae Brodkorb, 1971.

The two species from the Green River Formation fit well with Mayr's (1998) emended diagnosis of Primoscenidae, being small zygodactyl birds with a long, slender tarsometatarsus and a large processus intermetacarpalis of the carpometacarpus. Furthermore, the new species exhibit the apomorphies of the clade (*Primozygodactylus* + *Zygodactylus*) listed by Mayr (2008b): (1) trochlea metatarsi II of tarsometatarsus much shorter than trochlea metatarsi III and (2) with well-developed, plantarly projecting process, and (3) trochlea metatarsi IV with large trochlea accessoria, which is separated by a furrow from the trochlea metatarsi IV. According to Mayr (1998), the very long and slender tarsometatarsus that distinctly exceeds the humerus in length is another possible apomorphy of this clade, a character that is also found in the species described below.

Eozygodactylus n.gen.

Type species. *Eozygodactylus americanus* n.gen. and n.sp.

Etymology. *Eozygodactylus*—*Eos* Greek for dawn, *Zygodactylus*—for the zygodactyl foot.

Diagnosis. Within the Zygodactylidae, *Eozygodactylus* n.gen. is diagnosed as follows: (1) humerus with large processus supracondylaris dorsalis; (2) digitus minoris widens distally; and (3) pelvis with foramen obturatum open.

Character (1) is shared with *Zygodactylus* and a not yet named specimen from the London Clay held in a private collection (see also below); *Eozygodactylus* might be congeneric with the latter. Character (2) is autapomorphic for *Eozygodactylus*. Character (3) is plesiomorphic and also occurs in many other bird taxa such as e.g., Numididae, Charadriidae, Burhinidae, Rallidae, Phoenicopteridae, Threskiornithidae and Coraciidae, but not in *Primozygodactylus* (the pelvis is unknown for *Primoscens* and *Zygodactylus*).

Differential diagnosis. *Eozygodactylus* n.gen. differs from: (*a*) the Eocene *Primozygodactylus* Mayr, 1998 in: Scapula more strongly curved, humerus with smaller crista bicipitalis, carpometacarpus with larger difference in length between the ossa metacarpalia, sternum relatively longer craniocaudally; (*b*) the Eocene *Primoscens* Harrison & Walker, 1977 (the differential diagnosis is not only based on the holotype of *Primoscens minutus*, which only consists of a carpometacarpus, but also on specimen WN 87558A from the private collection of Michael Daniels that Mayr (1998) referred to the genus *Primoscens* [for figures, see Mayr, 1998: 78]) in: Humerus with processus supracondylaris (absent in cf. *Primoscens*), longer carpometacarpus (8.8 mm in *Eozygodactylus* versus 6.9 mm in *Primoscens*); and (*c*) the lower Oligocene–Miocene *Zygodactylus* Ballmann, 1971 in: Coracoid with medium-sized processus procoracoideus (absent in *Zygodactylus*), carpometacarpus with less difference in length between the ossa metacarpalia, legs relatively shorter.

Eozygodactylus americanus n.gen. and n.sp.

Holotype. USNM 299821, partial articulated skeleton lacking the pelvis and the legs (Fig. 9).

Type locality. Tynsky Quarry (F2), Kemmerer, Lincoln County, Wyoming, USA.

Type horizon. Tertiary, Eocene, Wasatchian, Green River Formation, Fossil Butte Member.

Paratype. WDC-CGR-014, articulated skeleton lacking the skull—the "skull" is painted by the preparator; from 18-inch-layer (Fig. 10).

Referred specimen. Tentatively referred: UWGM 40705, left wing, scapula, coracoid, parts of the sternum; from split-fish-layer.

Etymology. *americanus*—after *America*, the continent in which the Green River Formation is situated.

Diagnosis. As for genus.

Dimensions. See Table 4, 5 and 6.

Description. *Eozygodactylus americanus* resembles *Primozygodactylus danielsi* in its size and is thus one of the smaller species of the Zygodactylidae, but still larger than *Primoscens minutus*. Unless otherwise indicated, the description is mainly based on the USNM 299821 and WDC-CGR-014 specimens, since they are more complete and better preserved.

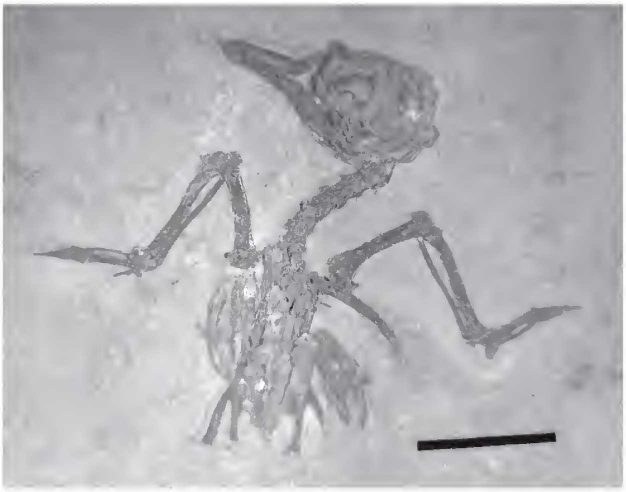

Figure 9. *Eozygodactylus wyomingensis* n.gen. and n.sp., holotype, USNM 299821, scale bar 20 mm.

The skull in USNM 299821 is slightly crushed, but some features may still be recognized. The prefrontal is not visible, it is either absent or hidden by the ripped and dislocated sclerotic ring. The preserved parts of the sclerotic ring do not allow detailed comparison with the sclerotic ring of *Primozygodactylus* (Mayr, 1998: fig. 21). With a length of approximately 13 mm, the maxilla is slightly shorter than that of *Primozygodactylus danielsi* (the two species have the same overall size). The narial opening is long, it measures about three quarters of the length of the maxilla. An ossified nasal septum does not seem to be present which is in accordance with *Primozygodactylus*, the Passeriformes and most Pici. The processus orbitalis of the quadratum is short in contrast to the elongated process of the Pici and Passeriformes.

As in *Primozygodactylus*, the symphysis mandibularis measures one fifth of the whole mandible. A groove is situated at the location where a fenestra mandibulae would otherwise be present.

The coracoid is long and slender, but neither the distal nor the proximal end are well enough preserved to show any details. A medium-sized processus procoracoideus is present (UWGM 40705). *Primozygodactylus* has a rather small processus procoracoideus, whereas cf. *Primoscens* has a very large processus procoracoideus (Mayr, 1998: fig. 22).

The scapula is bent more sharply than that of *Primozygodactylus*. The acromion is only moderately long and thus is similar to *Primozygodactylus danielsi*, whereas *Primozygodactylus major* has a very long acromion (Mayr, 1998: fig. 22).

The sternum resembles that of *Primozygodactylus* (Mayr, 1998: fig. 24), it is stocky, relatively short and mediolaterally broad. It is nearly as long as the humerus and, in relation to the wing, thus considerably longer than that of *Primozygodactylus danielsi*. The margo caudalis shows four incisurae, the incisurae laterales are deeper than the incisurae mediales. In *Eozygodactylus*, the trabeculae laterales and intermediales widen toward their caudal ends and reach further caudad than the trabecula mediana of the sternum. The trabeculae laterales reach even farther distad than the trabeculae intermediales. The spina externa is not visible in any specimen. The exact number of ribs is not determinable, at least four of them possess a processus uncinatus.

The humerus closely resembles that of Passeriformes. In accordance with WN 88583A and WN 92747 (collection Daniels from the London Clay, shown in Mayr, 1998: 79, pl. 7), the crista bicipitalis is only of moderate size, whereas *Primozygodactylus* has a pronounced crista bicipitalis. The tuberculum ventrale is prominent. The crista deltopectoralis of *Eozygodactylus* is low and short as in the other members

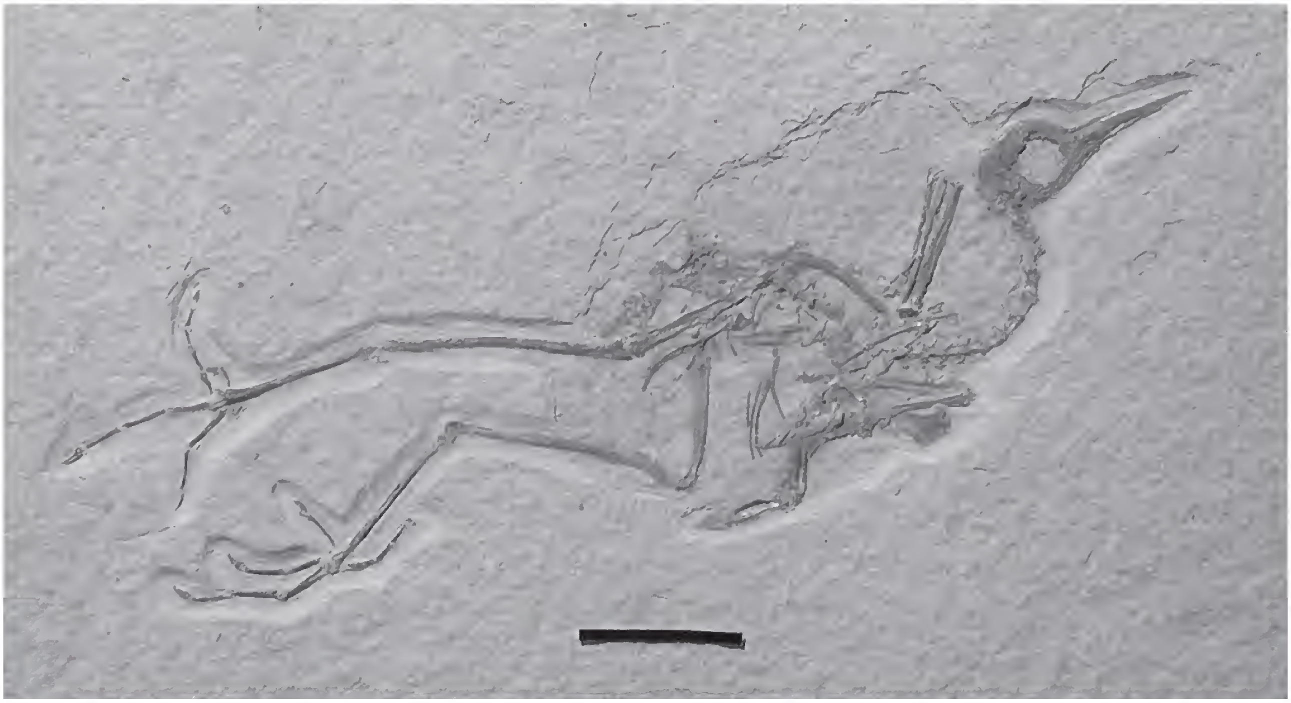

Figure 10. *Eozygodactylus wyomingensis* n.gen. and n.sp., paratype, WDC-CGR-014, scale bar 20 mm. The skull is fabricated.

Table 4. Green River Zygodactylidae, length of the limb bones, compared to *Primozygodactylus danielsi*, left/right, in mm (measurements of *Primozygodactylus danielsi* after Mayr, 1998).

	CO	HU	UL	CM	FE	TT	TM
Eozygodactylus americanus n.gen. and n.sp.							
USNM 299821	—	16.8/16.8	ca. 19/19.1	—/8.8	—	—	—
WDC-CGR-014	13.8/ca. 13.1	—/ca. 17.2	ca. 18.2/—	8.8/—	19.7/—	—/30.6	21.7/21.8
UWGM 40705	—	—	19.6	9.2	—	—	—
Zygodactylidae indet.							
NAMAL 2000-0217-004	10.5/—	13.5/ca. 13	18/18	7/ca. 7	—	19/20	14/14
BHI 1285	—	12.0/12.2	—	7.4/—	12.2/12.5	21.5/21.6	14.5/14.4
UWGM 21421	—	—	—	—	—/ca. 12	—/22	—/14.5
Primozygodactylus danielsi	13.5	16.7	19.0	8.4	16.9	27.9	20.0

of Zygodactylidae, it only measures about a fourth of the length of the humerus. The crista deltopectoralis approaches the shaft, whereas in *Primozygodactylus*, the crista is nearly parallel to the humerus shaft. As in *Primozygodactylus*, the shaft is only slightly curved. The apparently stronger curvature of the left humerus shaft in the USNM specimen is due to a fracture in the middle of the bone. The distal end of the humerus shows a pronounced processus supracondylaris dorsalis, which is similar in its size and location to that of the *Zygodactylus* and Passeriformes. *Primozygodactylus* and WN 87558A (cf. *Primoscens*) have a considerably smaller processus supracondylaris dorsalis (Mayr, 1998: fig. 25), which is oriented less proximad, but is perpendicular to the shaft. The fossa m. brachialis is moderately deep. As in *Primozygodactylus* and modern Piciformes, the ulna is longer than the humerus. The ratio humerus:ulna is concordant with that of *Primozygodactylus danielsi* and of *Primozygodactylus ballmanni*. However, the ulna is shorter than the tarsometatarsus in *Eozygodactylus*, whereas the two bones have nearly the same length in *Primozygodactylus*. In contrast to most Pici and many Passeriformes, the ulna lacks papillae remigiales. In *Primozygodactylus*, papillae remigiales are also absent. Neither the olecranon nor the distal end are discernible in any specimen. The carpometacarpus of *Eozygodactylus americanus* resembles closely that of *Primoscens* and of *Primozygodactylus*. The most conspicuous character is the large processus intermetacarpalis which reaches as far as to the os metacarpale minus, but is not fused to it. The os metacarpale minus is longer than the os metacarpale majus. The difference in length is larger than in *Primozygodactylus*. The proximal end of the carpometacarpus is only poorly preserved and thus allows few observations. The proximal end of the os metacarpale minus bears a slight tubercle, which probably corresponds to the "transverse ridge extending to the pisiform process" as described by Harrison (1982: 78). In how far this tubercle reaches the processus pisiformis is not visible in *Eozygodactylus*. A comparable tubercle is not visible in *Primozygodactylus*, but this might be due to preservation (Mayr, 1998). In *Eozygodactylus*, the processus extensorius is turned proximad to a greater extend than in *Primozygodactylus* (Mayr, 1998: fig. 26). As in *Primozygodactylus*, the synostosis metacarpalis distalis is broad. In contrast to *Primozygodactylus* (Mayr, 1998: fig. 26), the cranial margin of the os metacarpale majus is nearly straight and shows only a slight concave curvature. The phalanges match those of *Primozygodactylus*. The digitus alulae has only one phalanx. The distal phalanx of the digitus majoris is long and slender.

In contrast to *Primozygodactylus* and extant Passeriformes and Pici, the foramen obturatum is open caudally. In accordance with *Primozygodactylus*, the processus terminalis ischii is narrow and the distal end seems to be widened. The description of the legs is only based on the WDC specimen, since the other two specimens lack the hind limbs. As in *Primozygodactylus*, the tibiotarsus is by far the longest limb element. The distal condyles are craniocaudally deep and low, even lower than in *Primozygodactylus*. The tarsometatarsus is long and slender and in that respect resembles that of Passeriformes. Very few details are discernible at the proximal end, the hypotarsus seems to be small. The foramen vasculare distale is large and oval. In distal view, the trochleae are aligned as a curve, not planar like in passerines. The trochlea metatarsi III reaches considerably farther distad than the trochleae metatarsorum II and IV, which are approximately of the same length. The trochlea metatarsi II is only poorly preserved and a plantarly directing process is not visible. The fourth toe is opposed to the second and the third toe. All toes have the usual number of phalanges. The toes are longer than those of *Primozygodactylus* and have different proportions (tab. 5). The claws are short with a pronounced sulcus neurovascularis.

Table 5. *Eozygodactylus americanus* n.gen. and n.sp., specimen WDC-CGR-014, length of pedal phalanges, compared to *Primozygodactylus danielsi*, specimen SMF 2522, in mm (measurements of *Primozygodactylus danielsi* after Mayr, 1998).

	I1	I2	II1	II2	II3	III1	III2	III3	III4	IV1	IV2	IV3	IV4	IV5
Eozygodactylus americanus n.gen. and n.sp.														
WDC (left)	5.4	2.5	—	5.1	2.9	ca. 6.0	5.7	4.7	ca. 2.7	—	2.8	2.6	2.6	—
WDC (right)	ca. 5.6	ca. 2.0	5.9	5.2	ca. 2.2	ca. 4.6	5.7	4.8	3.3	2.7	2.9	2.6	2.6	—
Primozygodactylus danielsi														
SMF	4.0	2.4	4.8	4.3	2.4	5.7	4.9	4.3	2.6	2.9	2.9	2.5	2.5	2.0

Table 6. Green River zygodactylids, limb proportions compared to the Messel species of Zygodactylidae (measurements of *Primozygodactylus* after Mayr, 1998).

	HU:UL	HU:CM	HU:TM	UL:TT	UL:TM	CM:TM	TT:TM
Eozygodactylus americanus n.gen. and n.sp.							
USNM 299821	0.88	1.91	—	—	—	—	—
WDC-CGR-014	0.94	1.95	0.79	0.59	0.83	0.40	1.40
Zygodactylidae indet.	0.75	1.92	0.96	0.95	1.28	0.50	1.28
Primozygodactylus danielsi	0.88	2.13	0.89	0.72	1.02	0.42	1.43
Primozygodactylus major	0.92	2.24	1.03	0.79	1.11	0.46	1.41
Primozygodactylus ballmanni	0.88	2.23	0.84	0.72	0.95	0.38	1.33

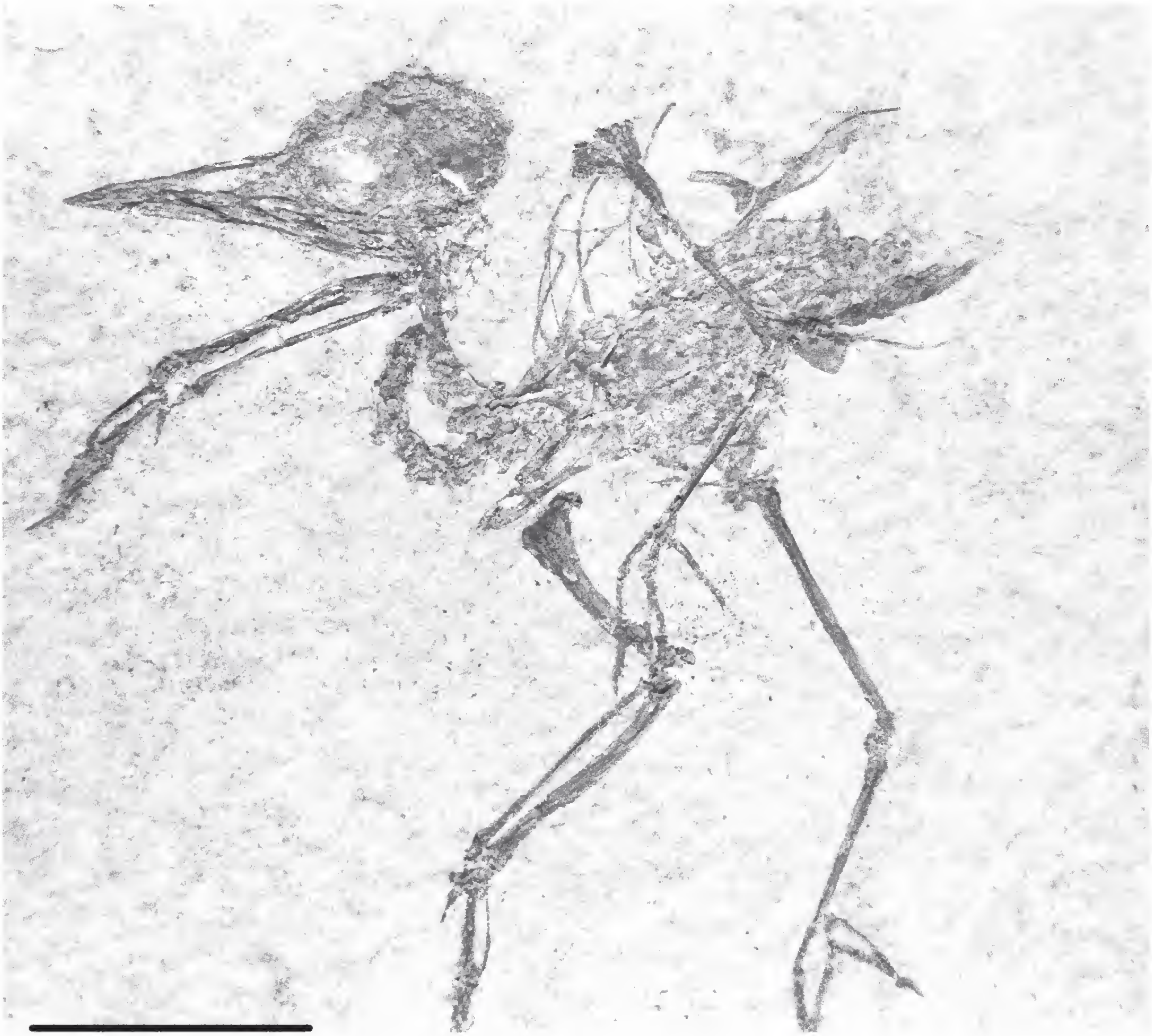

Figure 11. Zygodactylidae indet., NAMAL 2000-0217-004, scale bar 20 mm.

Zygodactylidae indet.

Besides *Eozygodactylus americanus*, a second species of Zygodactylidae occurs in the Green River Formation. It is represented by three specimens: BHI 1285, a complete articulated skeleton; NAMAL 2000-0217-004, also a complete articulated skeleton (Fig. 11) (the counterslab is in private hands and not available for study); and UWGM 21421, consisting of a right leg. These three specimens represent a new species, which differs from *Eozygodactylus americanus* in the following characters: (1) smaller overall size (length of tarsometatarsus 14.5 mm (BHI 1285) versus 21.7 mm in *Eozygodactylus americanus*) (Table 4, 6); (2) humerus with small processus supracondylaris dorsalis; (3) relatively longer ulna, which exceeds the tarsometatarsus in length.

In character (3), the undescribed species also differs from *Primozygodactylus*.

Because neither the BHI 1285 nor the NAMAL 2000-

0217-004 specimen were available for detailed studies, the new species is not named or described in detail. However, a few observations are made. The processus acrocoracoideus of the coracoid is large and hooked distally and resembles cf. *Primoscens* (WN 87558 collection Daniels). The processus procoracoideus is rather large, it seems to be somewhat relatively larger than that of *Eozygodactylus americanus* and clearly larger than that of *Primozygodactylus danielsi*. The extremitas omalis of the furcula is broad like that of *Primozygodactylus*, but contrary to the very narrow extremitas omalis of cf. *Primoscens* (Mayr, 1998: fig. 23). The humerus differs from that of *Eozygodactylus americanus*, but resembles that of *Primozygodactylus* in having a large crista bicipitalis. The processus supracondylaris seems to be considerably smaller than in *Eozygodactylus americanus* and thus is similar to *Primozygodactylus* and cf. *Primoscens* (Mayr, 1998: fig. 25).

Discussion. The fossil Zygodactylidae Brodkorb, 1971 are known from both complete articulated skeletons and three-dimensional preserved bones. Three genera have been described so far: *Zygodactylus* Ballmann, 1969 from the lower Oligocene to Miocene of Europe, originally known from distal tibiotarsi and tarsometatarsi (Ballmann, 1969a,b), until Mayr (2008b) described a new species based on a complete skeleton; *Primoscens* Harrison & Walker, 1977 and the taxon Primoscenidae from the Lower Eocene London Clay of England, was based on and only known from a single incomplete carpometacarpus (Harrison & Walker, 1977) until Mayr (1998) referred additional skeletal elements from the London Clay kept in a private collection; and *Primozygodactylus* Mayr, 1998 from the German Messel site was based on complete articulated skeletons (Mayr, 1998). The Primoscenidae were regarded as Passeriformes in the original description (Harrison & Walker, 1977), but their passeriform affinities were later doubted (Olson & Feduccia, 1979). The Messel specimens led Mayr (1998) to tentatively consider the Primoscenidae to be the sister group of a clade including the Miocene *Zygodactylus* and the Pici, mainly due to the presence of a zygodactyl foot with a trochlea accessoria (a sehnenhalter as described by Steinbacher, 1935). A first cladistic analysis including both the Primoscenidae and *Zygodactylus* resulted in a sister group relationship between the clade (Primoscenidae + Zygodactylidae) and Passeriformes (Mayr, 2004b). A new species of *Zygodactylus* showed the great similarities between *Zygodactylus* and Primoscenidae; in consequence, Mayr (2008b) synonymized Primoscenidae with Zygodactylidae. The new species of *Zygodactylus* also showed that zygodactylids are the sister taxon of Passeriformes (Mayr, 2008b).

From the Green River Formation, six specimens, which represent two species, were available for this study and are described above. In their overall appearance, the specimens from the Green River Formation closely resemble the Messel specimens. However, the Green River specimens can be distinguished from the Messel genus *Primozygodactylus*, mainly by characters of the humerus. Mayr (1998) mentioned several specimens from the London Clay (England) which are in the private collection of Michael Daniels. According to Mayr (1998), the specimens from the Daniels collection represent three different types of Zygodactylidae: One type probably belongs to the genus *Primozygodactylus*, one type represents the genus *Primoscens* and the third type "represents a not yet described genus" (Mayr, 1998: 51). This third type (Mayr, 1998: pl. 7) has a humerus that is very similar to that of *Eozygodactylus americanus* and may belong to the same genus. Both humeri exhibit a pronounced processus supracondylaris dorsalis at the distal end of the humerus, which is also found in some Passeriformes. The smaller species of Zygodactylidae from the Green River Formation differs in several aspects especially of the humerus from *Eozygodactylus americanus*. The humerus of the small Green River species resembles more closely that of cf. *Primoscens*, to which it also corresponds in size. However, it differs from cf. *Primoscens* in the shape of the extremitas omalis of the furcula. A closer study might reveal whether this small species is congeneric with one of the already described genera or if it represents a new genus of Zygodactylidae. Unfortunately, the characters listed by Mayr (2008b) as apomorphies for the clade (Zygodactylidae and Passeriformes) are not visible in any of the Green River specimens, with the exception of a well-developed processus acromialis, which is visible in the NAMAL specimen.

?Galbulae

"Neanis" kistneri (Feduccia, 1973)

Holotype. UWGM 3196, nearly complete articulated skeleton.

Referred specimen. USNM 336268, nearly complete articulated skeleton lacking the left foot (Fig. 12).

In its overall appearance and sitze, the referred specimen corresponds well with the holotype. The specimens share a large bicipital crest of the humerus, a carpometacarpus with straight ossa metacarpalia of identical length and a short synostosis metacarpalis distalis, and a zygodactyl foot with a strong third toe.

Dimensions. See Tables 7 and 8.

Description. The original description is based on the holotype only, given here are additional characters discernible on the referred specimen.

The exact shape of the skull is difficult to determine, because it is somewhat crushed. In accordance with *Galbula*, the os frontale is flat and a fossa temporalis is present. A small, slender piece of bone might represent the broken processus postorbitalis. If this identification is correct, the processus postorbitalis would have a length comparable to *Galbula*. The beak is nearly straight and slender, and shorter than that of Galbulidae. In the mandible, a fenestra caudalis mandibulae is visible.

Table 7. *"Neanis" kistneri*, length of limb bones, left/right, in mm.

	CO	HU	UL	CM	FE	TT	TM
UWGM 3196	11.6/ca. 10.7	17.3/ca. 16.7	20.1/—	9.1/—	—	20.8/20.5	11.5/11.5
USNM 336268	12.7/12.8	17.8/18.5	ca. 22.2/22.1	10.5/10.2	12.7/13.3	—/20.2	—/10.6

Table 8. *"Neanis" kistneri*, proportions of limb bones.

	HU:UL	HU:CM	HU:TM	UL:TT	UL:TM	CM:TM	TT:TM
UWGM 3196	0.86	1.90	1.50	0.97	1.75	0.79	1.81
USNM 336268	0.84	1.81	1.75	1.09	2.08	0.96	1.90

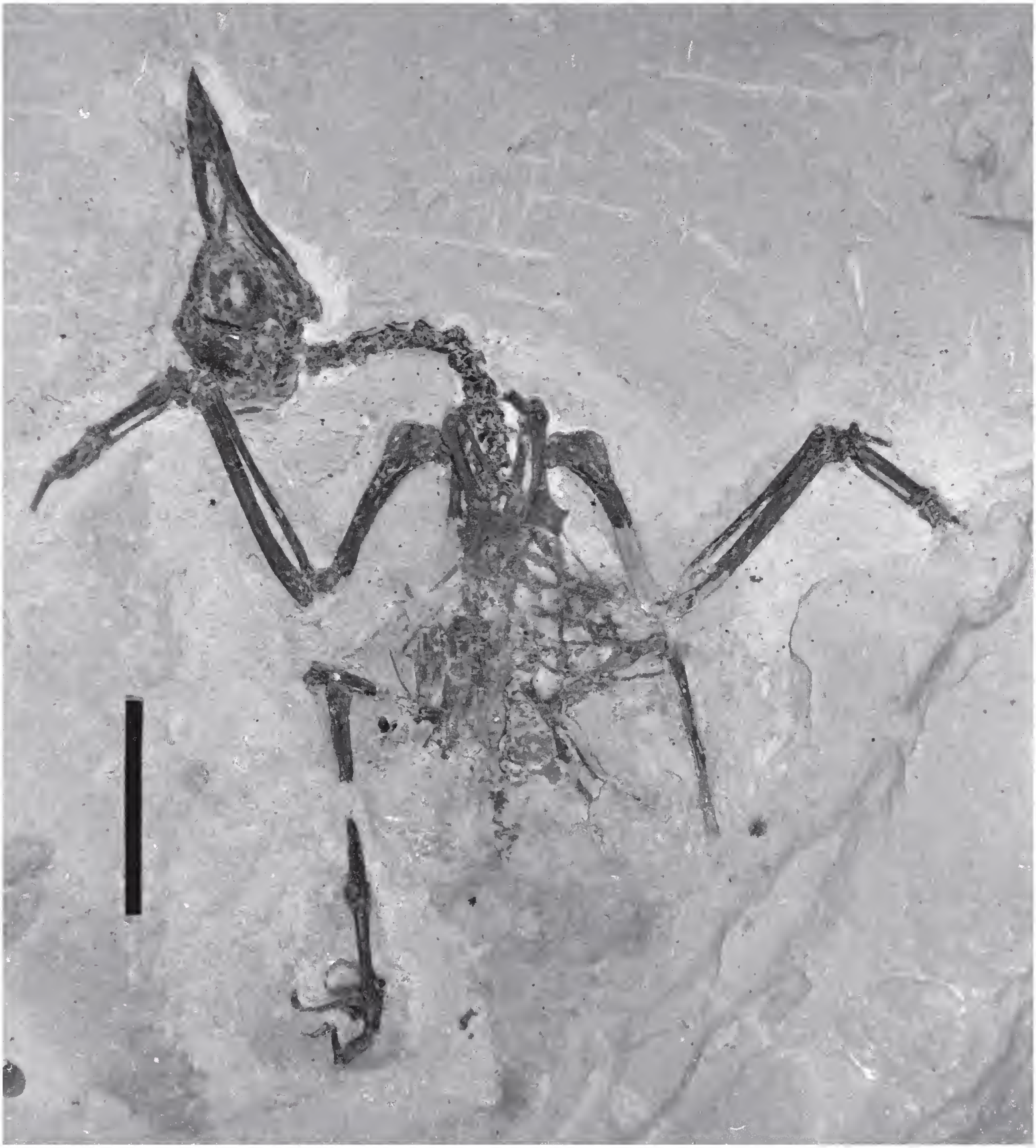

Figure 12. *"Neanis" kistneri*, USNM 336268, scale bar 20 mm.

The coracoid closely resembles that of *Primobucco mcgrewi*. The processus acrocoracoideus is large and slightly hooked, the processus procoracoideus is also large. In its shape, the processus lateralis resembles closely *Atelornis*. The facies articularis sterni is large like that of Galbulae and of Coraciiformes s.s. On the cranial side of the sternal end of the coracoid, a fossa is visible. A comparable fossa is present in Brachypteraciidae and some Bucconidae (*Bucco, Chelidoptera, Monasa*, and rather flat in *Malacoptila striata*). The furcula is rounded V-shaped, an apophysis furculae is not present.

The humerus resembles closely that of *Primobucco mcgrewi*. The head of the humerus is situated dorsally of the shaft due to the large crista bicipitalis. The crista deltopectoralis is short. The humerus shaft is slightly sigmoidal. The distal end is only poorly preserved and thus does not allow any detailed observations. The ulna is the longest limb element. In contrast to Galbulae, papillae remigiales are not present. The carpometacarpus is moderately long and slender. The ossa metacarpalia are parallel and have the same length. In contrast hereto, the os metacarpale minus is considerably longer than the os metacarpale majus within modern Galbulae. The processus extensorius is slightly turned proximad. The synostosis metacarpalis distalis is short.

Discussion. *"Neanis" kistneri* (Feduccia, 1973) was first described as *Primobucco kistneri*, a member of the Bucconidae (Feduccia, 1973). Together with three more genera, Feduccia & Martin (1976) then referred the species to the Primobucconidae, and transferred *Primobucco kistneri* to the genus *Neanis*. Houde & Olson (1989) regarded the Primobucconidae as a paraphyletic taxon and later referred several genera, which were originally placed into the Primobucconidae by Feduccia & Martin (1976), to the Sandcoleidae. Houde & Olson (1989) regard *"Neanis" kistneri* as "true member(s) of the Galbulae, as evidenced by the structure of the sehnenhalter of the tarsometatarsus" (Houde & Olson, 1989: 2031).

The holotype of *"Neanis" kistneri* clearly exhibits a truly zygodactyl foot with the fourth toe turned backwards and thus differs from the type species of the Primobucconidae, *Primobucco mcgrewi*, which is clearly anisodactyl and belongs to the Coraciiformes s.s. (Mayr *et al*., 2004).

The new specimen is better preserved than the holotype, however, only the dorsal side of the right tarsometatarsus is preserved. Thus, additional information on the sehnenhalter cannot be obtained. Nevertheless, *"Neanis" kistneri* exhibits further characters which it shares with the Galbulae as the shape of the skull, especially of the os frontale, the presence of a fossa temporalis, a large facies articularis of the coracoid and the head of the humerus turned medially. Due to these similarities and the presence of a zygodactyl foot with sehnenhalter, I concur with Houde & Olson (1989) that *"Neanis" kistneri* is indeed related to the Galbulae.

Conclusions

An extensive study of the Green River bird specimens revealed both new species such as the Zygodactylidae, as well as new specimens of already described species. The description of the majority of the bird species from the Green River Formation is based on single specimens. Most of these specimens are fairly complete, but severely crushed and thus reveal only limited information on their taxonomic affinities. Further specimens show important new features that allow new insight into the osteology of these species. For *Messelornis nearctica*, the new specimens show an amount of variation similar to the Messel species *Messelornis cristata*, and the description of *Messelornis nearctica* is revised in several characters. In the case of *Gallinuloides wyomingensis*, the additional data gained from the new specimen allows the recognition of its systematic position as a stem-group representative of the Galliformes (Mayr & Weidig, 2004). The systematic affinities of *"Neanis" kistneri* proposed by Houde & Olson (1989) are supported based on the new specimen.

The Green River Formation consists of deposits of three lakes which all yielded numerous fossils. The lakes range in age from the Upper Paleocene to the Middle Eocene (Grande, 1980). Most of the fossil birds were found in the Lower Eocene deposits of Fossil Lake. They are thus slightly older than the well-known avifauna from Messel (Germany). Many of the bird taxa known from Messel are now also reported from Green River and vice versa (e.g., Mayr, 2000; Mayr *et al*., 2004; Weidig, 2006). With over 340 described specimens, *Messelornis cristata* is by far the most abundant bird from Messel (Hesse, 1990). Until this study, *Messelornis nearctica* from Green River was only known from single specimen. The new specimens reported herein show that the Messelornithidae are among the most abundant species in Green River besides the Presbyornithidae (Feduccia & McGrew, 1975). In contrast hereto, with one respectively two known specimens, early galliforms seem to be rare in both sites. This might be due to different life habits, the early galliforms probably spent considerably less time close to the lakes than *Messelornis*. Messel is especially well known for its abundance of small arboreal birds such as Zygodactylidae, Messelirrisoridae or Gracilitarsidae (Mayr, 1998). With *Eozygodactylus americanus* and the un-named species, the first representatives of Zygodactylidae are now known from the New World. With a total of six specimens in two species, the Zygodactylidae are one of the more abundant avian taxa from the Green River Formation. They are also rather abundant in Messel with twelve specimens in four species (Mayr, 1998; Mayr & Zelenkov 2009). So far, early Galbulae are unknown from Messel or any other contemporaneous site in Europe and might be restricted to the New World.

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New Material of *Barawertornis tedfordi*, a Dromornithid Bird from the Oligo-Miocene of Australia, and its Phylogenetic Implications

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ABSTRACT. New fossil material of *Barawertornis tedfordi* (Aves: Dromornithidae) is described from Oligo-Miocene deposits in the Riversleigh World Heritage Area, northwestern Queensland, Australia. Phylogenetic analysis incorporating data from this new material casts some doubt on the generally accepted sister group relationship between *B. tedfordi* and all other dromornithids. However, the phylogenetic analysis is congruent with current hypotheses regarding intergeneric relationships among the other dromornithid taxa. A formal revision of dromornithid nomenclature that reflects these relationships is presented here. *Barawertornis tedfordi* may have closely resembled the unrelated Southern Cassowary *Casuarius casuarius* (Aves: Casuariidae), in that it was a rainforest-dwelling, flightless bird of similar size. *Barawertornis tedfordi* also appears to have had similar cursorial abilities to *C. casuarius*, based on its hind limb proportions.

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The Dromornithidae is an extinct family of large, flightless, terrestrial birds unique to Australia. It has one of the longest fossil records of any Australian group. These birds are known from the Late Oligocene to the Late Pleistocene, although an Early Eocene foot impression may be referable to Dromornithidae (Rich, 1979; Field & Boles, 1998; Miller *et al*., 1999; Vickers-Rich & Molnar, 1996; Boles, 2006). Dromornithids were traditionally thought to be ratites because they are superficially similar: large bodied, flightless birds with long necks, reduced wings, fused scapulocoracoids and acarinate sterna (Owen, 1872, 1874; Stirling & Zietz, 1896, 1900, 1905; Stirling, 1913; Rich, 1979, 1980; Jennings, 1990). This relationship was disputed by Olson (1985), based on observations of the mandible, quadrate and pelvis, and subsequently Vickers-Rich (1991) upon examination of newly prepared skulls from Bullock Creek, Northern Territory. Most recently, Murray & Megirian's (1998) phylogenetic analysis and re-evaluation of the skeleton concluded that dromornithids are part of the waterfowl radiation (Anseriformes).

Dromornithids are among the best represented fossil birds in Australia (Rich & van Tets, 1982; Murray & Vickers-Rich,

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2004). However, the five known genera and eight described species of dromornithid differ greatly in the extent of their representation by fossil material. Some species, such as *Genyornis newtoni* Stirling & Zietz, 1896 and *Dromornis stirtoni* Rich, 1979, are represented by cranial material and associated skeletons. Other species, such as *Barawertornis tedfordi* Rich, 1979, are known only from fragmentary and anatomically limited remains.

Barawertornis tedfordi is one of the earliest known dromornithids. It was first discovered in 1963 in Oligo-Miocene deposits in the Riversleigh World Heritage Area, northwestern Queensland, Australia (Tedford, 1968). Description of the genus and only known species by Rich (1979) was based on three hind limb fragments and a single dorsal vertebra from Riversleigh. Fragmentary tibiotarsi of *B. tedfordi* were briefly described by Murray & Vickers-Rich (2004), but little else that adds to our understanding of this species has been published.

In this paper, new hind limb material of *B. tedfordi* from Riversleigh is described. The anatomical information from this material is used to test the hypothesis that *B. tedfordi* is the sister group of all other dromornithids (Rich, 1979, 1980; Murray & Vickers-Rich, 2004). Previous conclusions about the intrafamilial relationships within Dromornithidae (Rich, 1979, 1980; Murray & Vickers-Rich, 2004) are also reassessed. Hypotheses regarding the overall biology of *B. tedfordi* are also presented, based on estimates of its body mass and its locomotory mode (as inferred from hind limb proportions).

Material methods

Comparisons of *Barawertornis tedfordi* were made with the following dromornithid taxa: *"?Bullockornis"* sp. Rich, 1979 (after Murray & Vickers-Rich, 2004); *Bullockornis planei* Rich, 1979; *Dromornis australis* Owen, 1872; *Dromornis stirtoni* Rich, 1979; *Genyornis newtoni* Stirling & Zietz, 1896; *"Ilbandornis?" lawsoni* Rich, 1979 (after Murray & Vickers-Rich, 2004); *Ilbandornis woodburnei* Rich, 1979. For clarity, the taxa *"?Bullockornis"* sp. and *"Ilbandornis?" lawsoni* are herein referred to as *Bullockornis* sp. and *Ilbandornis lawsoni*.

Measurements of specimens were made with digital calipers and rounded to the nearest 0.1 mm. A measuring tape was used for larger measurements. Measurements of specimens besides those of *B. tedfordi* were taken from the literature, if not indicated otherwise. Osteological terminology follows Baumel & Witmer (1993) and Ballmann (1969) with the following exceptions: the term "incisura tibialis lateralis" (="incisura tibialis" in Baumel & Witmer, 1993) is preferred to "ectocnemial channel" (Murray & Vickers-Rich, 2004), and "incisura tibialis medialis" is preferred to "entocnemial notch" (Murray & Vickers-Rich, 2004). "Eminentia cnemialis" would be the appropriate Latinized form for "cnemial eminence" (Murray & Vickers-Rich, 2004), as is "eminentia intercondylaris" for "intercondylar eminence" (Rich, 1979). Systematics follows Murray & Megirian (1998) and Murray & Vickers-Rich (2004).

Phylogenetic analysis. Additional character state scores for *B. tedfordi* were incorporated into Murray & Vickers-Rich's (2004) data matrix for species of dromornithids (see Appendix). These scores were determined from material described here and from vertebrae described by Boles (2000). The matrix of 40 characters and eight taxa was analysed with PAUP* 4.0b10 (Swofford, 2003).

It is uncertain which parsimony method Murray & Vickers-Rich (2004) used in their phylogenetic analyses, but examination of their character descriptions indicates that some multi-state characters represent plausible morphoclines and so can be ordered. We, therefore, conducted two phylogenetic analyses. In the first analysis, all characters were treated as unordered. In the second analysis, nine of the 40 characters were treated as ordered (see Appendix).

Dromornis australis was excluded from Murray & Vickers-Rich's (2004) full character matrix because it is known from only a right femur. To test the phylogenetic relationships of *D. australis* with other dromornithids, they analysed a data matrix of femoral characters only. We also analysed the femoral matrix, modified based on the new material of *B. tedfordi* described here, in order to evaluate the relative position of *D. australis* within Dromornithidae.

All tree searches used the branch and bound algorithm, which is guaranteed to find the most parsimonious trees. Tree length (L), consistency index excluding uninformative characters (CI), and retention index (RI) were calculated. To assess the robustness of clades, bootstrap support (Felsenstein, 1985) using 2000 replicates and Bremer support (Bremer, 1994) values were calculated. Following Murray & Vickers-Rich (2004), we used the Magpie Goose *Anseranas semipalmata* (Latham, 1798) as our outgroup because it is thought to be the most plesiomorphic living member of the Anseriformes.

Table 1. Measurements (mm) of femora referred to *Barawertornis tedfordi*.

QM F specimen	30352	39901	40231	40232	45056
length (caput femoris to condylus medialis)	—	—	>200.6	—	—
proximal width	—	ca. 82.1	ca. 89.0	ca. 89.1	>73.3
proximal depth	—	>41.4	—	—	—
depth of caput femoris	—	>27.4	ca. 32.7	35.2	—
minimum shaft width	—	—	—	—	ca. 35.5
minimum shaft depth	—	—	—	—	ca. 29.2
minimum shaft circumference	—	—	—	—	ca. 103.6
distal width	>76.3	—	—	—	—
depth of condylus medialis	>42.2	—	—	—	—
width of condylus lateralis	>20.4	—	—	—	—
depth of condylus lateralis	>56.3	—	—	—	—

Table 2. Measurements (mm) of tibiotarsi referred to *Barawertornis tedfordi*.

QM F specimen	30377	30801	30802	30828	45416	45417	52257	52260
length	—	—	—	—	>390.6	—	—	—
proximal width (caudal border)	—	—	ca. 66.5	>57.4	—	—	>55.9	—
proximal depth	—	—	—	>80.7	>72.5	>49.6	—	—
length of crista fibularis	—	—	—	—	—	—	>88.0	—
minimum shaft width	—	—	—	—	30.5	—	—	—
minimum shaft depth	—	—	—	—	24.7	—	—	—
distal width	>50.2	>47.4	—	—	ca. 50.9	—	—	>49.5
distal width across epicondylus medialis	—	>52.1	—	—	ca. 52.7	—	—	>53.1
depth of condylus medialis	>48.4	—	—	—	56.2	—	—	>48.3
depth of condylus lateralis	ca. 43.7	>41.7	—	—	48.2	—	—	>39.0
minimum length of pons supratendineus								
medial	15.5	—	—	—	10.5	—	—	13.4
lateral	14.2	—	—	—	13.8	—	—	13.3

Estimates of body mass and locomotion. The body mass of *B. tedfordi* was estimated using regression equations determined by Anderson *et al.* (1985) and Campbell & Marcus (1992) for birds (Table 1). Anderson *et al.*'s (1985) equation is based on the allometric relationship between body mass (M, in g) and mid-shaft circumference of the femur (MC_F, in mm):

$$M = 1.08 \times MC_F^{2.28 \pm 0.1} \qquad (1)$$

Campbell & Marcus's (1992) equations use least shaft circumferences of the femur (LC_F) and tibiotarsus (LC_T), which do not always coincide with the mid-shaft circumference:

$$\log_{10} M = 2.411 \times \log_{10} LC_F - 0.065 \qquad (2)$$

$$\log_{10} M = 2.424 \times \log_{10} LC_T + 0.076 \qquad (3)$$

Mid-shaft and least shaft circumferences of CPC7341 (holotype femur), QMF45056 (femur missing distal end) and QMF45416 (tibiotarsus missing proximal end) were measured using string and calipers. The body masses of other dromornithids and ratites were also estimated for comparison.

To gain insight into its locomotory mode, the hind limb bone ratio (lengths of femur: tibiotarsus: tarsometatarsus) of *B. tedfordi* was calculated and compared with those of other dromornithids and ratites.

Institutional abbreviations. CPC, Commonwealth Palaeontological Collections, Bureau of Mineral Resources, Canberra, Australia (now Geoscience Australia); QM F, Queensland Museum paleontological collections, Australia.

Geological setting

The specimens described here were recovered from Tertiary limestone deposits that crop out discontinuously within the Riversleigh World Heritage Area, in Lawn Hill National Park, northwestern Queensland, Australia. These deposits are interpreted to be part of Riversleigh Faunal Zones A and B (formerly "Systems" A and B; Arena, 2004; Travouillon *et al.*, 2006) and, as such, Late Oligocene-Early Miocene in age (Archer *et al.*, 1997; Arena, 2004; Travouillon *et al.*, 2006). Faunal Zone A sites are distinctive in that they include a higher proportion of aquatic fauna and large-bodied animals than do other sites at Riversleigh. The presence of large freshwater crocodiles, turtles, fish and frogs suggests that there were substantial pools of water supporting these animals. Pools of water were also present in Faunal Zone B sites, but were probably shallow or temporary because the few remains of smaller aquatic vertebrates recovered from these sites represent relatively small individuals (Archer *et al.*, 1989). Riversleigh's Oligo-Miocene paleoenvironments appear to have ranged from relatively open forests in the Late Oligocene to closed, species-rich gallery rainforest in the Early and Middle Miocene (Archer *et al.*, 1997; Travouillon *et al.*, 2009). The latter forests were probably similar to those of mid-montane New Guinea and perhaps not unlike the dense rainforests of northern Australia, New Guinea and adjacent islands in which the Southern Cassowary *Casuarius casuarius* (Linnaeus, 1758) lives today (Crome, 1975; Davies, 2002). For further information about locality and associated faunas, see Archer *et al.* (1997) and Travouillon *et al.* (2009).

Systematic paleontology

Order Anseriformes Wagler, 1831

Suborder Anhimae Wetmore & Miller, 1926

Family Dromornithidae Fürbringer, 1888

Barawertornis Rich, 1979

Type species. *Barawertornis tedfordi* Rich, 1979.

Diagnosis. As for the type species.

Age and distribution. Late Oligocene-Middle Miocene; Riversleigh World Heritage Area, northwestern Queensland, Australia. Murray & Vickers-Rich (2004) noted that a synsacral fragment and phalanges referable to *B. tedfordi* were found in the Early Miocene Leaf Locality at Lake Ngapakaldi, Tirari Desert, South Australia, but these materials have not yet been described.

Barawertornis tedfordi Rich, 1979

Figs 1–4

Holotype. CPC7341, a left femur missing the trochanter femoris and lateral part of the upper shaft.

Referred material. The following specimens were all collected from the Riversleigh World Heritage Area, Lawn Hill National Park, northwestern Queensland, Australia.

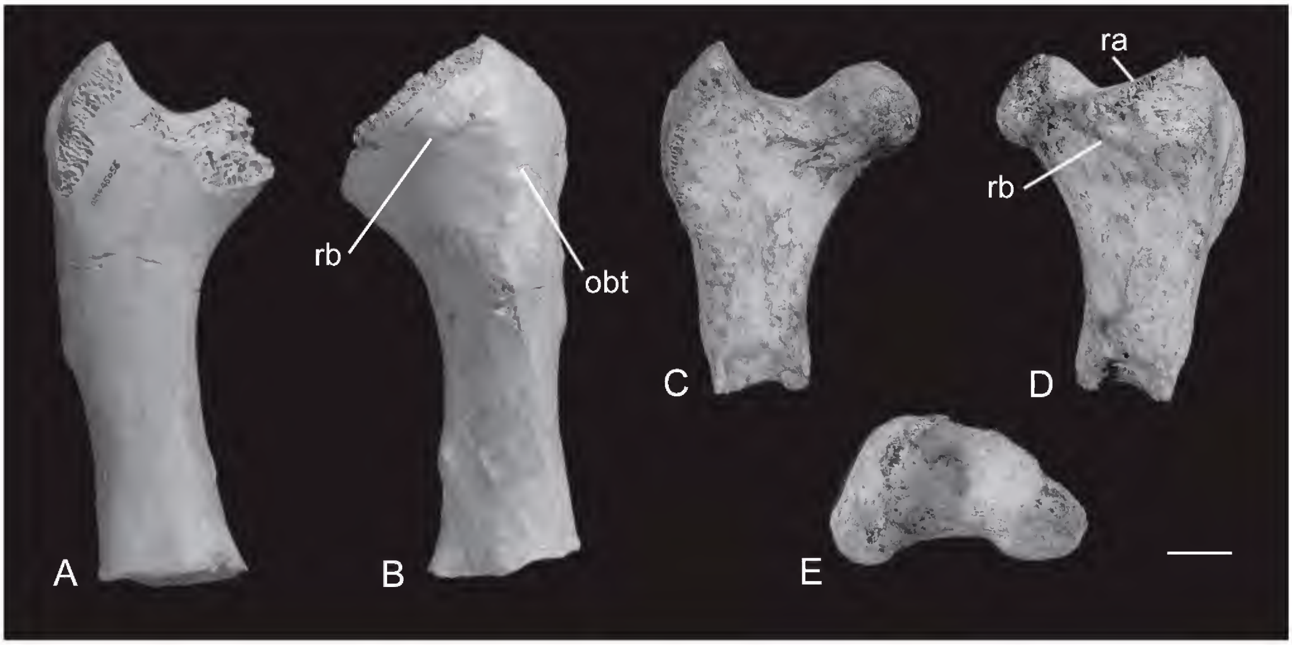

Figure 1. Specimens of *Barawertornis tedfordi*. (*A–B*) QM F45056, right femur missing distal third; (*A*) cranial view; (*B*) caudal view; (*C–E*) QM F39901, proximal end of right femur; (*C*) cranial view; (*D*) caudal view; (*E*) proximal view. Abbreviations: *ra* ridge A; *rb* ridge B; *obt* impressiones obturatoriae. Scale = 20 mm.

Localities are given in parentheses. *Femora*. QM F30352 (Wayne's Wok Site), distal end of left femur; QM F39901 (Upper Site), proximal end of right femur; QM F40231 (D Site), partial right femur; QM F40232 (Sticky Beak Site), proximal end of left femur; QM F45056 (Hiatus Site), right femur missing distal third; QM F45420 (Hiatus Site), shaft of right femur. *Tibiotarsi*. QM F30377 (White Hunter Site), distal end of right tibiotarsus; QM F30801 (White Hunter Site), distal end of left tibiotarsus; QM F30802 (White Hunter Site), proximal end of right tibiotarsus; QM F30828 (White Hunter Site), proximal end of left tibiotarsus; QM F45416 (Hiatus Site), left tibiotarsus missing proximal end; QM F45417 (Hiatus Site), proximal end of left tibiotarsus; QM F52257 (Lee Sye's Outlook Site), proximal half of right tibiotarsus; QM F52260 (Price Is Right Site), distal end of right tibiotarsus. *Tarsometatarsi*. QM F 24126 (Neville's Garden Site), distal end of right tarsometatarsus (trochleae metatarsi III and IV partially preserved); QM F30413 (Dirk's Towers Site), distal end of left tarsometatarsus (trochleae metatarsi II and III partially preserved); QM F45419 (Hiatus Site), heavily damaged right tarsometatarsus, broken into proximal and distal ends; QM F40223 (D Site), distal end of right tarsometatarsus; QM F40239 (Wayne's Wok Site), distal end of left tarsometatarsus (trochlea metatarsi IV partially preserved).

The following specimens of vertebrae, described by Boles (2000), were used for character scoring in phylogenetic analyses: QM F24377 (Neville's Garden Site), atlas-axis vertebral complex; QM F24378 (Neville's Garden Site), cervical vertebra.

Measurements. See Tables 1–3.

Type locality. D Site ("BMR Locality 103D" in Rich, 1979), Riversleigh World Heritage Area, Lawn Hill National Park, northwestern Queensland, Australia. Based on biostratigraphic and biocorrelative analyses, D Site forms part of Riversleigh's "Faunal Zone A", and as such is interpreted to be Late Oligocene in age (Archer *et al*., 1997; Arena, 2004; Travouillon *et al*., 2006).

Table 3. Measurements (mm) of tarsometatarsi referred to *Barawertornis tedfordi*.

QM F specimen	24126	30413	45419	52258	52259
length	—	—	>269.4	—	—
proximal width	—	—	62.4	—	—
dorsoplantar depth of cotyla medialis	—	—	23.7	—	—
dorsoplantar depth of cotyla lateralis	—	—	22.9	—	—
depth across area intercotylaris to hypotarsus	—	—	46.8	—	—
distal width	—	—	61.6	53.1	—
width of trochlea metatarsi II	—	>11.4	13.0	11.7	—
depth of trochlea metatarsi II					
medial	—	>17.3	17.9	20.1	—
lateral	—	>19.0	18.4	19.5	—
width of trochlea metatarsi III	26.1	>23.6	ca. 24.3	ca. 23.9	>23.8
depth of trochlea metatarsi III					
medial	—	—	32.0	>27.6	>34.4
lateral	31.8	—	30.3	ca. 32.5	>29.6
width of trochlea metatarsi IV	ca. 12.2	—	19.2	17.4	ca. 20.0
medial depth of trochlea metatarsi IV	>20.3	—	25.3	>22.3	ca. 27.1

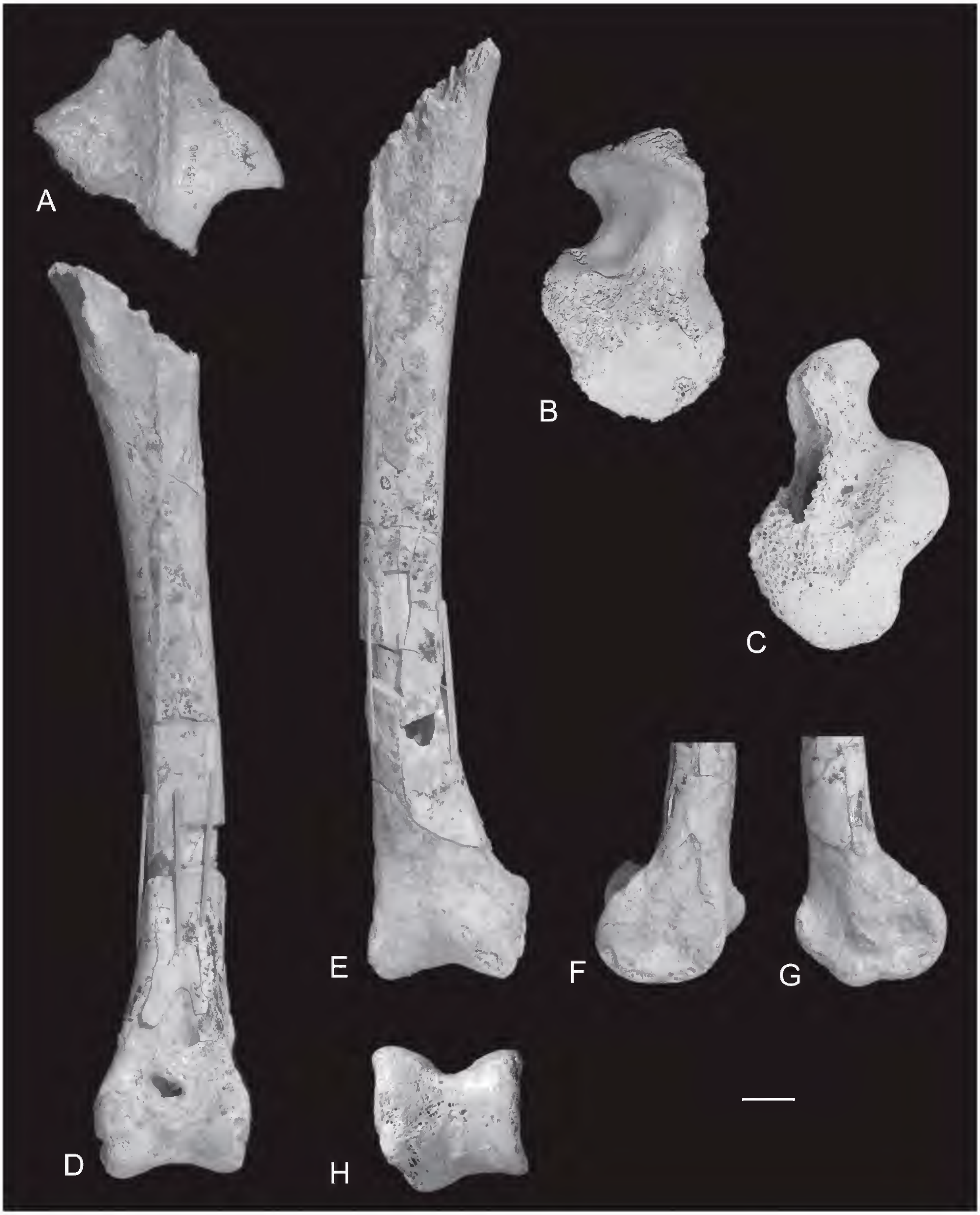

Figure 2. Specimens of *Barawertornis tedfordi*. (*A*) QM F45417, proximal end of left tibiotarsus, cranial view; (*B*) QM F30828, proximal end of left tibiotarsus, proximal view; (*C*) QM F30802, proximal end of right tibiotarsus, proximal view; (*D–H*) QM F45416, left tibiotarsus; (*D*) cranial view; (*E*) caudal view; (*F*) lateral view; (*G*) medial view; (*H*) distal view. Scale = 20 mm.
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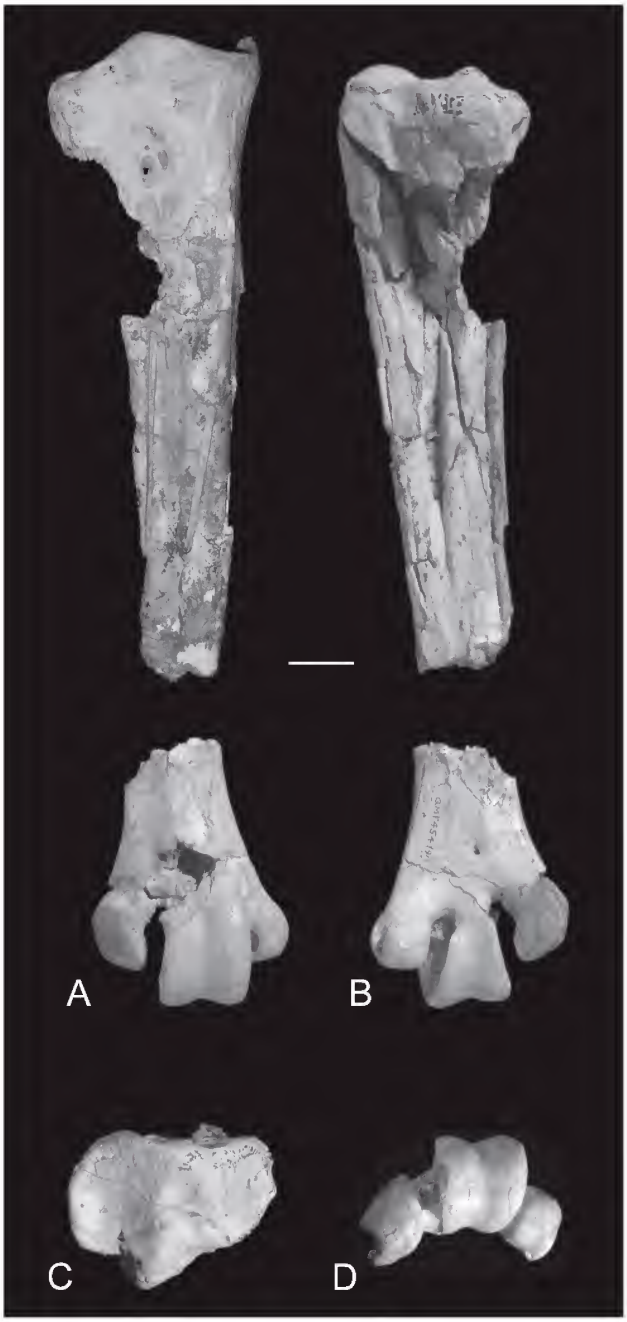

Figure 3. Tarsometatarsus of *Barawertornis tedfordi*. (*A–D*) QM F45419, right tarsometatarsus broken into proximal and distal ends; (*A*) dorsal view; (*B*) plantar view; (*C*) proximal view; (*D*) distal view. Scale = 20 mm.

Description

Femur. Description of the femur is based on new specimens, with reference to the holotype specimen CPC7341. The proximal and distal ends of the femur are not well preserved together in any the new specimens. As such, a comprehensive comparison of the proximal end with the distal end cannot be made. In cranial view the trochanter femoris is moderately high, narrow and falcate. It extends slightly laterad of the shaft. The proximal extent of the trochanter femoris and caput femoris are roughly equal. The caput femoris is relatively small in depth compared to *Genyornis* and *Dromornis*, with a slightly narrow, elongate collum femoris. The facies articularis antitrochanterica is highly concave both craniocaudally and mediolaterally in a broad U-shape. The fossa trochanteris is shallow. Viewed laterally, the trochanter femoris is largely oval-shaped. Its cranial margin is semicircular and extends slightly craniad of the shaft. The caudal margin of the trochanter femoris is almost straight and does not extend beyond the shaft surface.

In caudal view, a sharp ridge (A) is formed by the caudal border of the facies articularis antitrochanterica merging with the proximal crest of the trochanter femoris (Fig. 1D). Distal to ridge (A) is a second ridge (B), which extends from the caudal face of the trochanter femoris to the caput femoris. Ridge (B) occurs at an angle of about 45 degrees from the lateral shaft margin. In specimen QM F45056, ridge (B) trends at an angle of about 75 degrees from the lateral shaft margin. It joins to a broad, proximodistally trending ridge that may be interpreted as the impressiones obturatoriae (Fig. 1B). The length of the impressiones obturatoriae, seen in specimens QM F45056 and QM F40231, is less than half, but slightly more than one-third, of the total shaft length.

The shaft is shallow, craniocaudally compressed, and slender with respect to its length. In the holotype specimen CPC7341 the minimum width of the shaft is about 40 per cent of the distal end width. In CPC7341 and the new specimens the minimum shaft width is slightly proximad of its midpoint, with the exception of QM F40231—it is slightly distad. The cross-sectional shape of the shaft is roughly trapezoidal to elliptical. Viewed caudally, the medial shaft margin is slightly to moderately curved. The lateral shaft margin is more or less straight. In specimen QM F45056 the impressiones iliotrochantericae are prominent and broad, terminating proximad of the midpoint of the shaft long axis. The linea intermuscularis cranialis is prominent over the proximal one-third of the femur. It trends proximolaterally and forms an angle of about 5–10 degrees with the long axis of the shaft. The linea intermuscularis caudalis is prominent over the distal half of the femur, appearing narrower and sharper in the new specimens than in the holotype. It trends proximomedially and forms an angle of about 20–25 degrees with the shaft's long axis.

There is no linea intermusculus caudalis present in specimen QM F30352, but a small protuberance on the caudomedial margin. Lack of the linea intermusculus caudalis, unfused condyles, undeveloped popliteal fossa and porosity of the bone may indicate that this femur belonged to a young bird.

The condyli medialis et lateralis are not well preserved together in the new specimens. Although the condylus medialis is incomplete in specimen QM F40231, it appears to have a sharper caudal margin than that in the holotype.

Specimen QMF45420 bears a circular puncture hole of about 5 mm diameter on the cranial surface, mediad of the midline of the shaft (Fig. 4A). This unhealed puncture is associated with several greenstick fractures. Distal to the puncture are two smaller compression marks and a 2 mm long transverse gouge. These injuries indicate that they were formed at or near the time of death, possibly by a predator such as species of *Baru*; large, extinct freshwater crocodiles found at Riversleigh (see Geological Setting). Many fossil specimens of the dromornithid *Bullockornis planei* from the Bullock Creek locality in the Northern Territory bear tooth punctures and point fractures thought to be evidence of crocodile predation (Murray & Vickers-Rich, 2004).

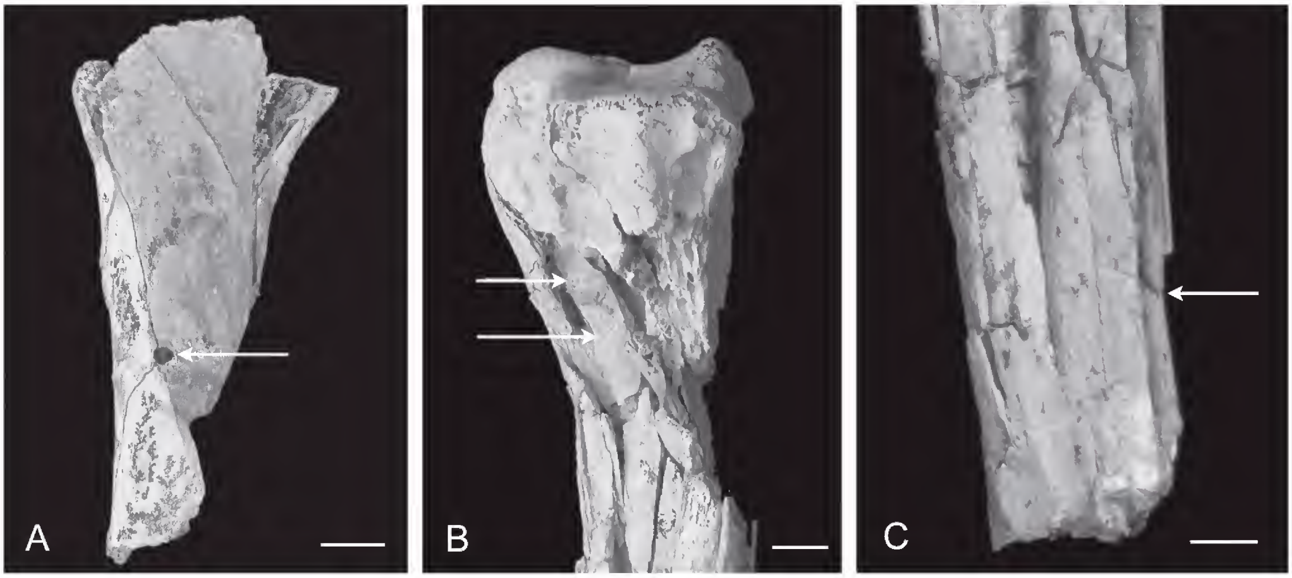

Figure 4. Specimens of *Barawertornis tedfordi*. (*A*) QM F45420, shaft of right femur, cranial view; (*B–C*) QM F45419, right tarsometatarsus; (*B*) caudal view of proximal end; (*C*) caudal view of distal third. Scale = 10 mm.

Tibiotarsus. In proximal view, the incisura tibialis lateralis is shallowly concave. The facies articularis lateralis is shallow and dome-like proximally. It extends slightly laterad and is semicircular in outline. The major axis of the facies articularis lateralis trends caudomedially. The facies articularis medialis is broadly convex, semicircular in outline and nearly flat proximally. From what is preserved, the eminentia intercondylaris appears to extend further proximally than the facies articularis lateralis. The fossa retropatellaris is circular and deep. The area interarticularis is moderately broad and concave proximolaterally. This entire surface slants distolaterally. The crista cnemialis lateralis is partially preserved. It is broad and triangular in cranial view, but is missing the proximal section of the crista. Only the base of the crista cnemialis cranialis is preserved. In proximal view the internal angle formed by the cristae cnemialis lateralis et cranialis is acute, approaching 90 degrees. The fossa flexoria is large and pneumatic. The impressio lig. collateralis medialis is distinct, large and elevated. It is deep and triangular in medial aspect.

The shaft is slightly curved mediolaterally. In caudal view, the medial margin of the shaft is more curved than the lateral margin. The caudal shaft surface is nearly planar but is slightly convex at the distal end. Over the proximal one-third, the cranial shaft surface is nearly planar and curves into the medial shaft surface. It smoothly grades into the lateral shaft surface that lies at about 90 degrees to the cranial shaft surface. The cranial and caudal shaft surfaces meet laterally along the crista fibularis at an angle of about 70 degrees in specimen QM F52257. In specimen QM F45416, these shaft surfaces meet laterally at about 110 degrees. In lateral view, the linea externa musculi peronei is broad and indistinct. Its proximal end is caudad to the crista fibularis. The linea externa musculi peronei trends distocranially and terminates proximad of the condylus lateralis. The linea extensoria is distinct; it trends distomedially away from the long axis of the shaft and intersects the medial shaft margin at about two-thirds down the shaft length. At the proximal and distal ends, the medial shaft surface is slightly convex. The remaining medial surface is nearly planar.

The distal end of the tibiotarsus is broad with respect to shaft width. The trochlea cartilaginis tibialis is moderately deep. The cristae trochleae are near vertical and do not converge proximally. Viewed cranially, the pons supratendineus forms an angle of about 75–85 degrees with the long axis of the shaft. The sulcus extensorius is deep. The distal opening of the canalis extensorius is slightly medial to the mediolateral midpoint of the distal end. The proximal margin of the area intercondylica is concave and forms a broad U-shape. The incisura intercondylaris is very shallow and broadly concave. It does not have an apex and is not V-shaped.

The condyli medialis et lateralis are moderately deep craniocaudally. Viewed cranially, the condyli are about equal in proximal extent. However, the condylus medialis is broader than the condylus lateralis. The proximal and distal margins of the condyli medialis et lateralis are slightly convex. In distal view the condyli appear to slightly diverge cranially, with the condylus medialis projecting further cranially than the condylus lateralis. It also projects further caudally than the condylus lateralis. From what is preserved, the condylus lateralis is roughly parallel with the shaft, whereas the condylus medialis is slightly inclined medially.

Viewed cranially, the condylus lateralis is relatively flat over its proximal half, but convex over its distal half. Its lateral margin is slightly convex and gradually grades into the lateral shaft margin. Viewed laterally, the condylus lateralis is broadly oval in shape. Its cranial margin is semicircular in outline, whereas its caudal margin is almost straight. The condylus lateralis projects a short distance caudad of the shaft but extends much further craniad. The distalmost extension of the condylus lateralis is at or craniad to its craniocaudal midpoint. The depressio epicondylaris lateralis is very shallow. The tuberculum retinaculi m. fibularis is small and slightly raised.

The condylus medialis is very convex over its cranial surface. Although its caudal and medial margins are damaged, the condylus medialis appears broadly oval in medial aspect. Its cranial margin is semicircular in outline. Viewed medially, there is a distinct distal protrusion from the distal margin of the condylus medialis (Fig. 2G), which is apparently absent in published specimens of other dromornithid species. This distal protrusion in *Barawertornis*, however, may be an artefact of the specimen's preservation. The depressio epicondylaris medialis is moderately deep. The epicondylus medialis is large, broad and circular. In caudal view the epicondylus medialis projects slightly further medially than the condylus medialis.

Tarsometatarsus. The proximal end of the tarsometatarsus appears to be relatively shallow compared to the shaft. Viewed proximally, the dorsal border of the proximal end is slightly convex, interrupted by the low eminentia intercotylaris. There is a shallow depression in the area intercotylaris. The hypotarsus is bulbous with a single poorly defined ridge. It is shaped like a scalene triangle, where the lateral side is more elongate than the medial side, and the dorsal side is the longest. Its proximal-most projection is located dorsally. There is a slight indentation in the lateral margin of the hypotarsus. In medial view, the hypotarsus moderately bulges plantarly beyond the shaft margin. The cotylae medialis et lateralis are narrow and roughly symmetrical. The cotyla medialis is moderately excavated, whereas the cotyla medialis is shallower and almost flat.

In dorsal view, the fossa infracotylaris dorsalis is narrow and moderately excavated. The foramina vascularia proximalia are large, deep and adjacent to each other. Distal to these foramina are two low, elongate tuberosities with a broad shallow groove between them; these are perhaps the insertions of the musculus tibialis cranialis. The impressiones retinaculi extensorii is shallow.

In all of the specimens under study, the proximal and middle shaft is not preserved or is heavily damaged. The medial shaft surface on the proximal half is discernable though; it is planar and meets the dorsal surface at about 90 degrees. Over the distal part of the shaft preserved, the dorsal shaft surface reveals a shallow sulcus extensorius extending from the damaged area. The sulcus extensorius appears to trend laterally, before terminating proximad of or level with the foramen vasculare distale. The medial and lateral margins of the sulcus flexorius are more prominent in the new specimens than in the paratype specimen CPC7346, described by Rich (1979). It is narrow and terminates proximad of or level with the foramen vasculare distale. In CPC7346, the cross-section of the shaft is teardrop-shaped, with the medial section of the shaft more circular in cross-section than the more triangular lateral section. In QM F52259, the cross-sectional shape of the shaft is oval, with the shaft dorso-plantarly compressed.

Viewed plantarly, the flare of the distal end is moderate to broad with respect to the shaft width. There is no distinct fossa metatarsi I. The foramen vasculare distale is absent in some specimens of *Dromornis stirtoni*, and its state is uncertain in *Bullockornis planei* (Rich, 1979). In *Barawertornis* it is present in specimens QM F40239 and QM F45419 but, due to damage, is not preserved in other specimens. This foramen is small and does not open into the incisura intertrochlearis lateralis. The incisura intertrochlearis lateralis is narrow and extends further proximad than incisura intertrochlearis medialis. The surface within the incisura intertrochlearis medialis slopes gradually to a shelf that forms about midway between the dorsal and plantar shaft surfaces.

Trochlea metatarsi II is nearly planar dorsally. Its dorso-plantar plane is tilted plantarly towards the lateral border. In medial view, the dorsal, distal and plantar margins of this trochlea are smoothly rounded and approach a semicircular outline. Its medial face is moderately to deeply excavated. Viewed distally, the medial and lateral margins of trochlea metatarsi II diverge plantarly. The dorsal margin of trochlea metatarsi II is about three-quarters the width of the plantar margin.

Dorsal projection of trochlea metatarsi III with respect to the other two trochleae is moderate to great. The central axis of trochlea metatarsi III is slightly mediad to that of the shaft. Only trochlea metatarsi III bears a trochlear groove on the articular surface. This groove is shallow, and is of same depth dorsally and plantarly. In lateral view, the trochlea metatarsi III is circular in outline and has a large, moderately deep depression on its lateral face. In medial view, this trochlea is oval-shaped and has a small and moderately deep depression. The plantar margin of trochlea metatarsi III projects further beyond the shaft than its dorsal margin. Viewed distally, the medial and lateral margins of this trochlea diverge plantarly, and its plantar margin is about three-quarters of the width of the dorsal margin.

In dorsal view, the articular surface of trochlea metatarsi IV is nearly planar, with its plane tilted plantarly towards the lateral border. The dorsal, distal and planar margins of the trochlea form a semicircle in lateral view. Its most plantar projection is distad of the proximal end of the plantar margin.

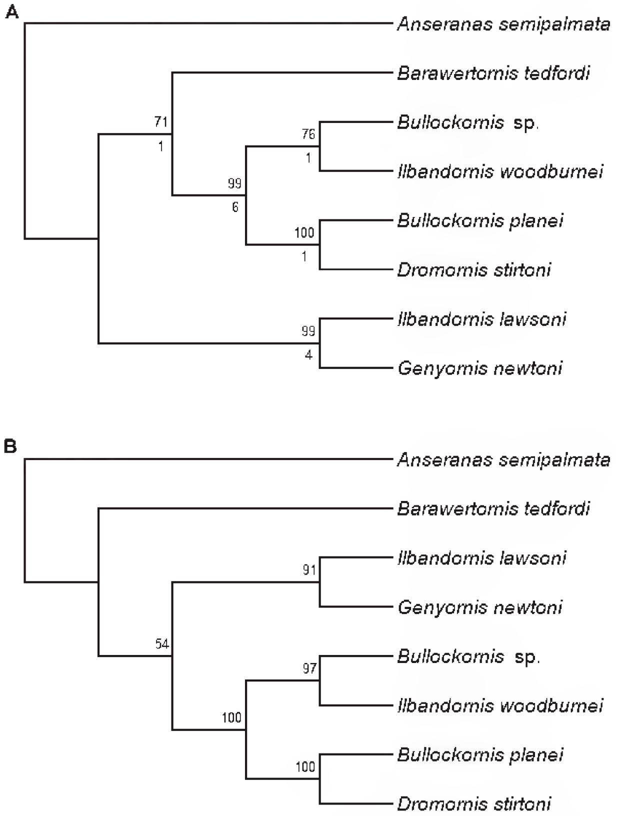

Figure 5. Phylogenetic hypotheses of intrafamilial relationships within the Dromornithidae. (*A*) Single most parsimonious tree resulting from unordered analysis. Bootstrap values are indicated above branches; Bremer support values are indicated below branches. This tree topology was also derived in ordered analysis. (*B*) One of two equally parsimonious trees resulting from ordered analysis. Bootstrap values are indicated above branches.

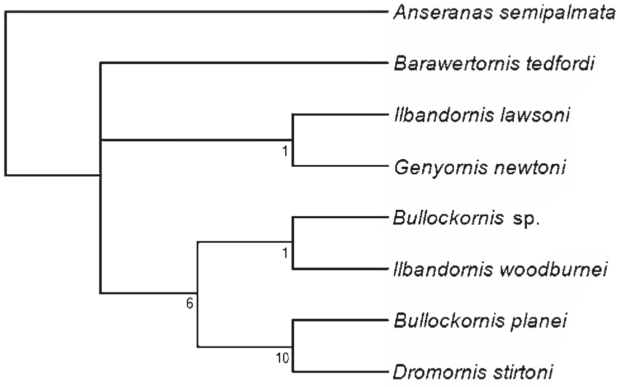

Figure 6. Strict consensus tree of two equally parsimonious trees resulting from ordered analysis. Bremer support values are indicated below branches.

There is a deep depression in the lateral surface of trochlea metatarsi IV. Viewed distally, the dorsal and plantar margins of this trochlea converge laterally. The medial margin is slightly convex and the lateral margin is highly concave.

There is a series of diagonal gouges present on the posterior surface of a heavily damaged right tarsometatarsus (QMF45419, Fig. 4B). Distad to these gouges, another transverse gouge is present (Fig. 4C). These markings may have been inflicted by a predator or a scavenger post-mortem, or animals trampling on the bone.

Results and phylogenetic analysis

Analysis of unordered characters. Analysis of 40 unordered characters resulted in one most-parsimonious tree (Fig. 5A; L = 60, CI = 0.92, RI = 0.93). This tree is consistent with that produced by Murray & Vickers-Rich (2004) in that it supports the monophyly of a group comprising *Bullockornis* sp., *Ilbandornis woodburnei, Bullockornis planei* and *Dromornis stirtoni*, and the clades identified within it. The *Ilbandornis lawsoni-Genyornis newtoni* clade is also proposed in this tree. Species of *Ilbandornis* and *Bullockornis* are divided between different clades.

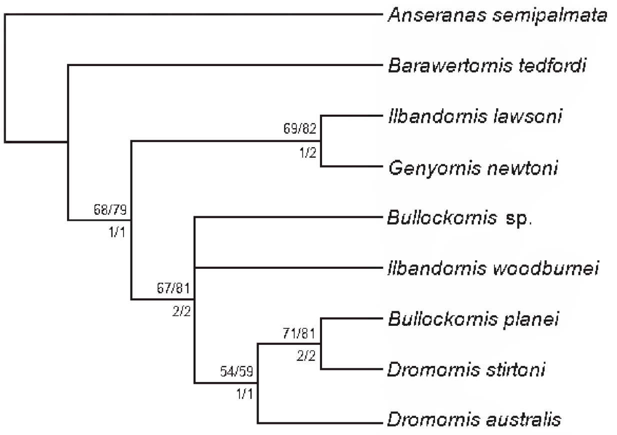

Figure 7. Phylogenetic hypothesis of dromornithid relationships resulting from analysis of femoral characters only. Bootstrap values are indicated above branches; Bremer support values are indicated below branches. Support values to the left are from unordered analysis; values to the right are from ordered analysis.

The position of *Barawertornis tedfordi* in this tree, however, differs from that proposed in previous studies. Here, *B. tedfordi* is the sister group to the clade comprising *Bu.* sp., *I. woodburnei, B. planei* and *D. stirtoni*. Together, these five species form a clade to the exclusion of *I. lawsoni* and *G. newtoni*. However, this clade receives relatively weak bootstrap and Bremer support (Fig. 5A).

The clade comprising of *B. tedfordi, Bu.* sp., *I. woodburnei, B. planei* and *D. stirtoni* is supported by the following synapomorphies: strongly convex culmen and deep and compressed beak (unknown for *B. tedfordi, Bu.* sp., *I. woodburnei*); deep ramus mandibulae (unknown in *B. tedfordi, Bu.* sp.); derived states of the ventral crests and median surface of synsacrum (varies within group, unknown in *Bu. planei*); derived states of crista patellaris of tibiotarsus (varies within group); transversely wider proximal articular surface of tarsometatarsus (plesiomorphic in *Bu.* sp., *I. woodburnei*). All of these character states are not homoplasious relative to large body size.

Analysis of ordered characters. Analysis of nine ordered and 31 unordered characters (see Appendix) resulted in two equally parsimonious trees (L = 65; CI = 0.85; RI = 0.87). The topology of the first tree, tree A, is the same as that derived in the unordered analysis (Fig. 5A). The topology of the second tree, tree B, (Fig. 5B) is identical to the original tree proposed by Murray & Vickers-Rich (2004), in which *B. tedfordi* is sister group to all other dromornithids. The bootstrap consensus tree generated also had the latter topology.

The two topologies resulting from the ordered analysis agree on the monophyly of *Bu.* sp., *I. woodburnei, Bu. planei* and *D. stirtoni*, and the relationships within this clade. They also agree on the grouping of *I. lawsoni* and *G. newtoni*. However, they disagree on the phylogenetic position of *B. tedfordi* relative to the other dromornithid species (Fig. 5A–B).

The synapomorphies that unite *B. tedfordi* with *Bu.* sp., *I. woodburnei, Bu. planei* and *D. stirtoni* in tree A are identical to those that unite the same group in the unordered analysis. The synapomorphies that unite the other dromornithids to the exclusion of *B. tedfordi* in tree B are as follows: sulcus intercondylaris of femur a wide right angle or obtuse angle (varies within group, plesiomorphic in *I. lawsoni*); large fossa poplitea; constricted eminentia cnemialis (extent varies within group); incisura tibialis lateralis is deep open notch; shallow, concave incisura tibialis medialis; very asymmetrical trochlea cartilaginis tibialis. These features, however, appear to correlate with large body size. This clade receives low bootstrap support (Fig. 5B).

A strict consensus tree based on the results of the ordered analysis is given in Fig. 6, with *B. tedfordi* forming an unresolved trichotomy with the *I. lawsoni–G. newtoni* clade and that of the other dromornithid species.

Analysis of femoral characters only. Analysis of this matrix recovered the same single most-parsimonious tree, irrespective of whether characters were unordered or ordered (unordered: L = 15, CI = 0.83, RI = 0.85; ordered: L = 16, CI = 0.80, RI = 0.83) (Fig. 7). This tree topology is identical to that derived by Murray & Vickers-Rich (2004), except that the branches leading to *Bu.* sp. and *I. woodburnei* are collapsed. These two species do not form a clade because they have identical femoral character states but there are no synapomorphies linking them. *Barawertornis tedfordi* remains the sister group to the other dromornithid species. *Dromornis australis* appears to be more closely related to *D. stirtoni* and *Bu. planei* than the other dromornithids.

Diagnoses of clades excluding *Barawertornis tedfordi*. In the following, synapomorphies that diagnose clades excluding *Barawertornis tedfordi* are listed. These only include synapomorphies exhibited in all clade members and in all analyses.

The clade consisting of *Bu.* sp., *I. woodburnei, Bu. planei* and *D. stirtoni* is diagnosed by the following synapomorphies: deep ramus mandibulae (unknown in *Bu.* sp.); deep and bulky condylus lateralis of femur; condylus medialis much deeper craniocaudally than condylus lateralis of tibiotarsus; deep, hatchet-shaped and near vertical crista cnemialis lateralis; deep, open incisura tibialis lateralis; shallow, concave incisura tibialis medialis; depressio epicondylaris medialis of tibiotarsus depressed by tuberosity; very asymmetrical trochleae cartilaginis tibialis.

The *Bu.* sp.–*I. woodburnei* clade is diagnosed by the following synapomorphies: very constricted eminentia cnemialis; acute angle between cristae cnemialis cranialis et lateralis; narrow, elongated proximal surface of tibiotarsus; proximal margin of condylus lateralis of tibiotarsus is broad, low and moderately prominent laterally; cristae trochleae of tibiotarsus are shallow and deviated laterally.

The *Bu. planei–D. stirtoni* clade is diagnosed by the following synapomorphies: strongly convex culmen, deep and compressed beak; fused atlas-axis complex; wider than long vertebrae cervicales; wide, obtuse sulcus intercondylaris of femur; slightly constricted eminentia cnemialis; crista patellaris is thick triangular tuberosity; broad, oval proximal surface of tibiotarsus; incisura intercondylaris is wide V-shape with acute apex; obliquely oval and elongated distal condylus lateralis of tibiotarsus; oblique, flange-like cristae trochleae; trochlea metatarsi II longer than IV; foramen vasculare distale low, within trochlear notch; wide incisurae intertrochlearis; deep and dorsally prominent trochlea metatarsi III.

The *I. lawsoni–G. newtoni* clade is diagnosed by the following synapomorphies: trochanter femoris considerably higher than the caput femoris; moderately constricted eminentia cnemialis; deep, almost circular incisura tibialis lateralis; marked reduction of trochlea metatarsi II; trochlea metatarsi II shorter than IV.

The *Bu. planei–D. stirtoni–D. australis* clade is diagnosed by oblique cristae sulci patellaris and wide sulcus patellaris of femur.

Body mass and hind limb proportions

Body mass estimates. The estimated body masses of dromornithids and other large flightless birds are presented as an order of magnitude in Tables 4–5. *Barawertornis tedfordi* was the lightest known dromornithid species. Its estimated body mass, using Campbell & Marcus's (1992) regression equations, is about 59–64 kg. Using Anderson *et al.*'s (1985) equation, the estimated mass range for *B. tedfordi* is about 27–79 kg, and the mean mass 46 kg. The maximum body mass estimated for *B. tedfordi* is within the minimum range of *D. australis. Barawertornis tedfordi* weighed approximately half that estimated for *I. lawsoni* and *Bu.* sp. The other dromornithid species were more heavily built, similar to the Elephant Bird *Aepyornis maximus* Geoffroy Saint-Hilaire, 1851, and moa *Pachyornis elephantopus* (Owen, 1856). *Dromornis, B. planei, G. newtoni* and *I. woodburnei* are within the mass range calculated for moa species *Dinornis giganteus* (*sensu* Jennings, 1990) and *Dinornis maximus* (*sensu* Stirling & Zietz, 1900; Alexander, 1983). The specimens of the latter species, however, are now known to represent the largest female South Island Giant Moa *Dinornis robustus*, the only member of the genus on the South Island of New Zealand (Bunce *et al.*, 2003; Worthy *et al.*, 2005). The largest of the dromornithid species, *D. stirtoni*, weighed almost ten times more than *B. tedfordi*.

The estimated body masses of the extant ratites we obtained (Tables 4–5) are mostly within the observed ranges recorded in Davies (2002) and Dunning (2008). The minimum and maximum mass estimates for the Ostrich *Struthio camelus* Linnaeus, 1758, Emu *Dromaius novaehollandiae* (Latham, 1790), and Southern Cassowary *Casuarius casuarius* are slightly outside the observed ranges. The estimated body mass range for the Dwarf Cassowary *Casuarius bennetti* Gould, 1857 is below the observed mass recorded in Diamond *et al.* (1999).

In comparison to extant flightless birds, *B. tedfordi* was lighter than *S. camelus*. The lower body mass estimates for *B. tedfordi* are within the ranges observed in the Greater Rhea *Rhea americana* (Linnaeus, 1758), *D. novaehollandiae, C. bennetti* and *C. casuarius*. Its mean mass estimates are closest to the maximum mass recorded for *C. casuarius*.

Murray & Vickers-Rich (2004) estimated the body masses of dromornithid species and other birds using a regression equation from Anderson *et al.* (1985) for bipedal dinosaurs rather than birds (equation 1 in Methods). It appears that they inadvertently used least shaft circumferences, not mid-shaft circumferences, to obtain their estimates from Anderson *et al.*'s (1985) equation. They also estimated masses using Campbell & Marcus's (1992) regression equation based on femur circumference. However, they unintentionally converted the original log 10 equation (equation 2 in Methods) to the following non-log equation:

$$\text{Weight} = -\,0.065 \times (\text{femur circumference})^{2.411}$$

The correct non-log equation is:

$$\text{Weight} = 10^{-0.065} \times (\text{femur circumference})^{2.411}$$

After substituting Murray & Vickers-Rich's (2004) circumference measurements in their non-log equation and Campbell & Marcus's (1992) original log equation, different body mass estimations were obtained. It is uncertain how Murray & Vickers-Rich (2004) obtained their estimations from this equation, but their values overestimate the body masses of dromornithids, especially for the heavier birds. Using the correct equation from Campbell & Marcus (1992) and Anderson *et al.*'s (1985) equation for birds, we recalculated body mass estimates for the other dromornithids (Tables 4–5).

Hind limb proportions. Unfortunately, none of the new specimens of *Barawertornis tedfordi* preserves the complete lengths of the femur, tibiotarsus and tarsometatarsus. To estimate its hind limb bone ratio, we used the maximum length of the tarsometatarsus (QM F45419) and the internal length (caput femoris to condylus medialis) of the femur

Table 4. Body mass estimates of *Barawertornis tedfordi* based on femora (holotype CPC7341 and QM F 45056) compared to estimates for other dromornithids and flightless birds. Nomenclature of moa species follows source authors. Mass estimates were calculated using the mid-shaft circumference (MC_f) equation from Anderson *et al.* (1985) [a], and the least shaft circumference (LC_f) equation from Campbell & Marcus (1992)[b]. See Methods for regression equations. Circumference measurements are given as mean (minimum-maximum) values. N/A = not available.

species	source	MC_f (mm)	mass based on MC_f (kg)	LC_f (mm)	mass based on LC_f (kg)
Barawertornis tedfordi	this study	107.3 (104–110.6), n = 2	x = 46 (28.8–73.5) min = 42.9 (26.9–68.2) max = 49.3 (30.8–79)	101.6, n = 1	59.4
Bullockornis sp.	Murray & Vickers-Rich (2004)	N/A	N/A	140 (139–141), n = 2	x = 128.6 min = 126.4 max = 130.8
Bullockornis planei	Murray & Vickers-Rich (2004)	N/A	N/A	207.3 (186–220), n = 6	x = 331.4 min = 255.2 max = 382.5
Dromornis australis	Stirling & Zietz (1900)	171, n = 1	133.2 (79.7–222.8)	N/A	N/A
Dromornis stirtoni	Jennings (1990); Murray & Vickers-Rich (2004)	N/A	N/A	249.8 (210–285), n = 17	x = 519.5 min = 341.9 max = 713.9
Genyornis newtoni	Stirling & Zietz (1900)	228.7 (218–234), n = 3	x = 258.6 (150.2–445.1) min = 231.8 (135.3–397.1) max = 272.4 (157.9–470.1)	N/A	N/A
Ilbandornis lawsoni	Murray & Vickers-Rich (2004)	N/A	N/A	142 (134–155), n = 3	x = 133.1 min = 115.7 max = 164.4
Ilbandornis woodburnei	Murray & Vickers-Rich (2004)	N/A	N/A	176.5 (160–193), n = 2	x = 224.9 min = 177.5 max = 278.9
Dinornis maximus [c]	Stirling & Zietz (1900)	240, n = 1	288.6 (166.8–499.3)	N/A	N/A
Pachyornis elephantopus	Stirling & Zietz (1900); Jennings (1990)	196, n = 1	181.9 (107.3–308.3)	167.5 (160–175), n = 2	x = 198.2 min = 177.5 max = 220.3
Aepyornis maximus	Stirling & Zietz (1900)	270, n = 1	377.5 (215.7–660.8)	N/A	N/A
Struthio camelus	this study	143 (133–145), n = 3	x = 88.6 (54–145.6) min = 75.1 (46.1–122.5) max = 91.5 (55.6–150.5)	137.3 (133–143), n =3	x = 122.7 min = 113.7 max = 135.4
Dromaius novaehollandiae	this study	93.8 (92–95), n = 5	x = 33.9 (21.5–53.4) min = 32.4 (20.6–51) max = 34.9 (22.1–55)	92.2 (91–93.5), n = 5	x = 47 min = 45.5 max = 48.6
Rhea americana	this study	74 (73–75), n = 2	x = 19.7 (12.8–30.4) min = 19.1 (12.5–29.4) max = 20.3 (13.2–31.3)	73.5 (73–74), n = 2	x = 27.2 min = 26.8 max = 27.7
Casuarius bennetti	this study	76, n = 1	21 (13.6–32.3)	73, n = 1	26.8
Casuarius casuarius	Anderson *et al.* (1985); W. Longmore (pers. comm.); R. Palmer (pers. comm.)	94, n = 1	34.1 (21.6–53.6)	92.3 (78–103), n = 4	x = 47.1 min = 31.4 max = 61.4

[a] Anderson *et al.* (1985) regression equation gives estimate ranges of body mass. Presented here are the calculated mass and estimate range based on the mean (x), minimum and maximum circumference values.

[b] Campbell & Marcus's (1992) regression equation gives single-figure estimates of body mass. Here we present the mean (x), minimum and maximum mass values calculated from the mean, minimum and maximum circumference values.

[c] *Dinornis maximus* is synonymized under *Dinornis robustus* in current nomenclature (Bunce *et al.*, 2003).

Table 5. Body mass estimates of *Barawertornis tedfordi* based on the tibiotarsus (QM F45416) compared to estimates for other dromornithids and flightless birds. Nomenclature of moa species follows source authors. Body mass estimates were calculated using the least shaft circumference (LC_t) equation from Campbell & Marcus (1992)[a] (equation 3 in Methods). Measurements are presented as mean (minimum–maximum).

species	source	LC_t (mm)	mass based on LC_t (kg)
Barawertornis tedfordi	this study	89.3 n = 1	63.8
Dromornis stirtoni	Jennings (1990)	207.3 (200–220) n = 4	x = 491.4 min = 450.5 max = 567.6
Ilbandornis lawsoni	Jennings (1990)	110 n = 2	105.8
Ilbandornis woodburnei	Jennings (1990)	113.3 (108–120) n = 4	x = 113.6 min = 101.2 max = 130.6
Dinornis giganteus [b]	Jennings (1990)	150 n = 1	224.3
Pachyornis elephantopus	Stirling & Zietz (1900); Jennings (1990)	146 (125–162) n = 5	x = 210.1 min = 144.2 max = 270.3
Aepyornis maximus	Stirling & Zietz (1900)	155 n = 1	242.9
Struthio camelus	this study	107 (98–113) n = 3	x = 98.9 min = 79.9 max = 112.9
Dromaius novaehollandiae	this study	75.6 (71–81) n = 5	x = 42.6 min = 36.6 max = 50.4
Rhea americana	this study	64 (63.5–64.5) n = 2	x = 28.5 min = 27.9 max = 29
Casuarius casuarius	R. Palmer (pers. comm.); this study	87.7 (86–91) n = 3	x = 61.1 min = 58.2 max = 66.8

[a] Campbell & Marcus's (1992) regression equation gives single-figure estimates of body mass. Here we present the mean (x), minimum and maximum mass values calculated from the mean, minimum and maximum circumference values.

[b] Jennings (1990) measured specimens of *Dinornis giganteus* from the South Australian Museum collection. All of the *D. giganteus* specimens in the South Australian collection were found on the South Island of New Zealand (T.H. Worthy, pers comm.), and would therefore be synonymized under *Dinornis robustus* in current nomenclature (Bunce *et al*., 2003).

(holotype CPC7341). The tibiotarsal length was calculated by adding the maximum length of QM F45416, a left tibiotarsus missing the proximal end, and the maximum length of QM F45417, proximal end of a left tibiotarsus. QM F45416 and QM F45417 were recovered from the same limestone block and are probably fragments of the one tibiotarsus.

The hind limb bone ratio derived for *B. tedfordi* was about 1:1.9:1.2. A ratio of approximately 1:2:1 is also seen in *Bu. planei, D. stirtoni, G. newtoni* and *Dinornis. Pachyornis elephantopus*, and all other non-dinornithid moa, and *A. maximus* had relatively shorter tarsometatarsi in comparison to the femur. *Ilbandornis lawsoni* had a relatively long tarsometatarsus, with a hind limb bone ratio of about 1:2:2, like in *S. camelus, D. novaehollandiae* and *R. americana* (Table 6).

Discussion

Phylogenetic relationships. Two phylogenetic hypotheses of the intrafamilial relationships within the Dromornithidae have been produced in our analyses. In both, the relative phylogenetic positions of *I. lawsoni, G. newtoni, Bu.* sp., *I. woodburnei, Bu. planei* and *D. stirtoni* remain the same. In all analyses, a monophyletic group comprising *Bu.* sp., *I. woodburnei, Bu. planei* and *D. stirtoni* is present. Within this group the pairs of *Bu.* sp. and *I. woodburnei*, and *Bu. planei* and *D. stirtoni* form subclades. The phylogeny based on only femoral characters suggests that *D. australis* is most closely related to *Bu. planei* and *D. stirtoni*. Outside this monophyletic group, *I. lawsoni* and *G. newtoni* also form a clade. These relationships are consistent with those proposed by Murray & Vickers-Rich (2004).

However, our results provide conflicting data about the relative position of *B. tedfordi* within the Dromornithidae. One hypothesis suggests that *B. tedfordi* is the sister taxon to all other dromornithids (Fig. 5B), as initially proposed by Rich (1979) and supported by Murray & Vickers-Rich (2004). This is driven by retention of plesiomorphic features in *B. tedfordi* including a small fossa poplitea, no constriction of the eminentia cnemialis, a shallow incisura tibialis lateralis, and absence of an incisura tibialis medialis.

The alternative hypothesis suggests that *B. tedfordi* is the sister group to the monophyletic group comprising *Bu.* sp., *I. woodburnei, Bu. planei* and *D. stirtoni,* to the exclusion of *I. lawsoni* and *G. newtoni* (Fig. 5A). This relationship has not been suggested before, and is based on information provided by the new fossil material of *B. tedfordi* described here. The synapomorphies linking these taxa (see Results) do not appear to be homoplasious with respect to large body size, and hence are likely to be of great phylogenetic significance.

However, both hypotheses regarding the position of *B. tedfordi* are weakly supported, as indicated by the relatively low bootstrap and Bremer support values (Figs 5A,B). Thus

Table 6. Hind limb bone ratios (lengths of femur: tibiotarsus: tarsometatarsus) for *Barawertornis tedfordi* and other dromornithids. Ratios of other flightless birds are also shown for comparison. Nomenclature of moa species follows authors. It is uncertain in the literature if the given bone lengths of fossil birds are from articulated or isolated bones. Here we treated bone lengths of fossil birds as measurements of isolated bones, and calculated ratios using the minimum and maximum known lengths.

species	source		bone length (mm)			ratio
			F	TBT	TMT	
Barawertornis tedfordi	this study		226.2	>430.5	>269.4	1:1.9:1.2
Bullockornis planei	Murray & Vickers-Rich (2004)		350	600[a]	390	1:1.7:1.1
Dromornis stirtoni	Jennings (1990);	min	330	750	406	1:2.3:1.2
	Murray & Vickers-Rich (2004)	max	470	830	465	1:1.8:1
Genyornis newtoni	Stirling & Zietz (1900);	min	322	602[b]	320	1:1.9:1
	Rich (1979)	max	345	602[b]	379	1:1.7:1.1
Ilbandornis lawsoni	Jennings (1990);	min	290	425	475[b]	1:1.5:1.6
	Murray & Vickers-Rich (2004)	max	325	540	475[b]	1:1.7:1.5
Ilbandornis woodburnei	Murray & Vickers-Rich (2004)	min	260	570[b]	340	1:2.2:1.3
		max	290	570[b]	360	1:2:1.2
Dinornis giganteus[c]	Jennings (1990)		406	889	495	1:2.2:1.2
Dinornis maximus[c]	Alexander (1983)		404.9	859	451.9	1:2.1:1.1
Pachyornis elephantopus	Jennings (1990)		317.9	545.6	233.6	1:1.7:0.7
Aepyornis maximus	Jennings (1990)		480	640	330	1:1.3:0.7
Struthio camelus	this study		317	525	447	1:1.7:1.4
Struthio camelus	Gatesy & Biewener (1991)		294	524	474	1:1.8:1.6
Dromaius novaehollandiae	this study		229	455	381	1:2:1.7
Dromaius novaehollandiae	this study		230	437	403	1:1.9:1.8
Dromaius novaehollandiae	this study		242	464	413	1:1.9:1.7
Dromaius novaehollandiae	Jennings (1990)		203	401	383	1:2:1.9
Rhea americana	Jennings (1990)		220	330	324	1:1.5:1.5
Rhea americana	Gatesy & Biewener (1991)		210	319	306	1 :1.5:1.5
Casuarius casuarius	R. Palmer (pers. comm.)		261	421	331	1:1.6:1.2
Casuarius casuarius	Jennings (1990)		264	443	323	1:1.7:1.2

[a] Length is estimated from specimens of similar sized individuals.

[b] The same value is used to calculate both minimum and maximum ratios. This is because only one specimen is known for the species, or only one measurement is noted in the literature (though there may be more than one specimen described).

[c] See footnotes for Tables 4–5 for explanation of current *Dinornis* nomenclature.

the strict consensus tree based on these two hypotheses represents our preferred summary of dromornithid intrafamilial relationships (Fig. 6) based on current material, with a trichotomous relationship between *B. tedfordi*, the *I. lawsoni–G. newtoni* clade and all other dromornithids. This tree confirms the repeatedly recovered inter-relationships among all other dromornithids found in the other trees, but reflects the uncertain position of *B. tedfordi* within the family.

Resolution of conflict about the intrafamilial position of *B. tedfordi* is impeded by the limited characters available for phylogenetic analyses. At present, the hind limb is the only complete character system available for comparison across all dromornithid taxa. The discovery of more complete fossil material from different morphological (character) systems is needed to further understand the relationships between *B. tedfordi* and other dromornithids, and/or definition of new characters of the known skeletal elements.

Recommended changes to taxonomy. The current analyses support data presented by Murray & Vickers-Rich (2004), and indicate that a formal revision of dromornithid nomenclature is required to reflect the phylogeny. *Bullockornis* sp. and *Ilbandornis lawsoni* were provisionally allocated to these genera by Rich (1979) based on the very little material known at the time, but the current study shows that they appear to be more closely related to other genera. A close relationship between *I. lawsoni* and *G. newtoni* is supported by a number of shared derived states and high bootstrap and Bremer support values (Figs 5 and 7). This suggests that these species are congeneric and hence *Ilbandornis lawsoni* should be renamed *Genyornis lawsoni*, as that generic name has priority.

There is also strong evidence that *Bu.* sp. and *I. woodburnei* belong to the same genus, based on high bootstrap and Bremer support values and several synapomorphies of the tibiotarsus (Fig. 5). The femoral character states for *Bu.* sp. and *I. woodburnei* are identical and do not vary from the states of the node shared with *Bu. planei, D. stirtoni* and *D. australis*. These could therefore be interpreted as ancestral states for the *Bu. planei–D. stirtoni–D. australis* group in which derived states occur (Fig. 7). In order to indicate the close relationship between *Bu.* sp. and *I. woodburnei, Bu.* sp. should be assigned to *Ilbandornis*. It has no specific name because it has not been formally described.

Table 7. List of all dromornithid taxa and their revised names, in accordance to phylogenetic relationships evident in analyses.

dromornithid species	revised name
Barawertornis tedfordi	—
"?*Bullockornis*" sp.	*Ilbandornis* sp.
Bullockornis planei	*Dromornis planei*
Dromornis australis	—
Dromornis stirtoni	—
Genyornis newtoni	—
"*Ilbandornis*?" *lawsoni*	*Genyornis lawsoni*
Ilbandornis woodburnei	—

Bullockornis planei appears to be more closely related to *D. stirtoni* than to *Bu.* sp. The two species share many synapomorphies of the cranial and postcranial skeleton, and their relationship is strongly supported by significantly high bootstrap and Bremer support values (Figs 5–7). We argue that *Bu. planei* and *D. stirtoni* are probably part of a temporal series and should be considered as congeneric; thus *Bullockornis planei* should be renamed *Dromornis planei*.

However, the genus *Dromornis* is problematic because of the paucity of material representing its type species, *D. australis*. The lack of representation for this species makes it uncertain that *D. stirtoni* is correctly assigned to this genus. This can only be confirmed with discovery of more fossil material for *D. australis* and consequent reanalysis of dromornithid intrafamilial relationships.

Although the above relationships were also found by Murray & Vickers-Rich (2004), these dromornithid species were still maintained in separate genera. We consider that the taxonomic revision presented here, which reflects the phylogenetic relationships within the Dromornithidae, is necessary to improve our understanding of the taxonomy of the group; hereafter in this paper, dromornithid taxa are referred to by their revised names (following Table 7).

Paleobiology. *Barawertornis tedfordi* was the smallest of the known dromornithids, with an estimated body mass range of 26.9–79 kg, and mean mass of 46–63.8 kg. This bird was smaller than *S. camelus*, and is within the higher mass ranges observed in *D. novaehollandiae, R. americana*, and *C. bennetti*. It is most similar in size to *C. casuarius*. Its femur is proportionately short and stout relative to that of *S. camelus* and *D. novaehollandiae*, but is gracile in comparison to the more robust femora of other dromornithids, dinornithiforms and *A. maximus*.

Cursoriality in animals is associated with an increase in lengths of the distal limb elements relative to the proximal ones (Howell, 1944; Storer, 1960; Gray, 1968). This overall increase of the distal limb elements, as well as elongation of the tarsometatarsus relative to the tibiotarsus, is exhibited in cursorial ground birds such as *S. camelus, D. novaehollandiae* and *R. americana* (Gatesy & Biewener, 1991; Boles, 1997, 2001; Christiansen & Bonde, 2002). The hind limb proportions of *Genyornis lawsoni* are very similar to those of these birds, suggesting that this species was also capable of running at rapid speed over long distances. Relative proportions of the hind limb bones in *B. tedfordi*, however, are most similar to that of *C. casuarius. Casuarius casuarius* is less cursorial than *S. camelus, D. novaehollandiae* and *R. americana*, but has powerful legs capable of sustaining a reasonable degree of speed if required (Boles, 1997). This suggests that *B. tedfordi* exhibited similar cursorial abilities.

The hind limb bone ratios obtained for dromornithid and other fossil taxa are derived from bones of different individuals. Inferences of their locomotory mode are based on observations of living, unrelated animals. As such, these inferences are speculative and should be treated with caution.

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Appendix

Character state scores for *Barawertornis tedfordi* in the matrix of Murray & Vickers-Rich (2004).

	1	1111111112	2222222223	3333333334
	1234567890	1234567890	1234567890	1234567890
Barawertornis tedfordi	??00???010	0000000000	0000100?00	0000000100

Characters 13, 16–17, 21–22, 25, 27, 30 and 32 were ordered in the second phylogenetic analysis (see Methods). The femoral matrix was derived from scores for characters 10–18.

Notes. In their analysis, Murray & Vickers-Rich (2004) scored the hind limb bone ratio (character 11) and the proximal articular surface of the tarsometatarsus (character 38) of *B. tedfordi* as 0 (plesiomorphic). However, it is not clear whether this scoring was based on observations of fossil material (rather than assumed), because there is no indication in their descriptions that the tibiotarsal length or proximal tarsometatarsus were known for *B. tedfordi* at the time. We scored character 38 as 1 for *B. tedfordi* based on observations of specimen QM F45419; however, this state may be exaggerated by the distortion and poor preservation of the bone. Because the complete lengths of the tibiotarsus and tarsometatarsus are unknown for *B. tedfordi*, we used the minimum lengths of these bones and the internal length of the femur to score character 11. This character was scored as 0 for *B. tedfordi*.

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A New Cormorant-like Bird (Aves: Phalacrocoracoidea) from the Early Miocene of Rauscheröd (Southern Germany)

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Abstract. Presented here is a new species of a cormorant-like bird, assigned to ?*Borvocarbo tardatus* n.sp., from the Early Miocene of the locality Rauscheröd in Southern Germany. The preserved bones, a tibiotarsus, fragmentary ulna and radius, are compared in detail to those of fossil and extant taxa of phalacrocoracoids. Provided that the generic affiliation is confirmed when additional material is discovered, the new species is the stratigraphically youngest evidence and representative of the genus *Borvocarbo*.

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Cormorants are aquatic, piscivorous, diving birds of the Old and New World. Today they are most diversified in the Southern Hemisphere, where they inhabit both marine and freshwater environments. The fossil record of Phalacrocoracoidea (cormorants and anhingas, sensu Livezey & Zusi, 2007) dates back until the Early Oligocene of Europe (e.g., Mourer-Chauviré *et al.*, 2004; Rasmussen *et al.*, 1987; Roux, 2002), perhaps even to the Late Eocene (Mourer-Chauviré *et al.*, 2004); however, the oldest systematically determinable genera/species are described from the Late Oligocene (Mayr, 2007; Mourer-Chauviré *et al.*, 2004).

Tertiary taxa of European Phalacrocoracoidea belong to six genera: *Borvocarbo* Mourer-Chauviré, Berthet & Hugueney, 2004 (Late Oligocene and Early Miocene [this paper]), *Phalacrocorax* Brisson, 1760 (Early Miocene–Recent), *Oligocorax* Lambrecht, 1933 (Early Miocene), *Nectornis* Cheneval, 1984 (Miocene), and *Limicorallus* Kurochkin, 1968 (Late Oligocene and Early Miocene) and, as the single representative of darters, *Anhinga* Brisson, 1760 (Late Miocene–Recent). The fossil representatives of the genera *Phalacrocorax, Oligocorax, Nectornis* and *Limicorallus* are accepted as members of the Phalacrocoracidae (cormorants), whereas, following Mayr (2007), ?*Borvocarbo stoeffelensis*, and hence the entire genus, is probably phylogenetically positioned outside of the crown group (Phalacrocoracidae+Anhingidae), but still a Phalacrocoracoidea.

Hitherto, 11 species of cormorants and cormorant-like taxa are known during the Late Oligocene and Miocene in Europe (Table 1). Fossil darters are represented in Europe only by *Anhinga pannonica* (Lambrecht, 1916) from the Late Miocene of Romania (MN10) and Austria (MN9); this species has also been reported from the Late Miocene of Tunisia (Rich, 1972).

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Table 1. Valid fossil species of cormorants and its kin known from the Late Oligocene and Miocene in Europe.

Borvocarbo guilloti Mourer-Chauviré, Berthet & Hugueney, 2004	Late Oligocene	France
?*Borvocarbo stoeffelensis* Mayr, 2007	Late Oligocene (MP30)	Germany
Oligocorax littoralis (Milne-Edwards, 1863)	Early Miocene (MN1–3)	France, Germany, Czechia
Phalacrocorax intermedius (Milne-Edwards, 1867–1871a)	Early and Middle Miocene (MN3–5)	France, Germany, Czechia
Phalacrocorax ibericus Villalta, 1963	Late Miocene (MN9)	Spain
Phalacrocorax lautus Kurochkin & Ganea, 1972	Late Miocene (MN9?)	Moldova
Phalacrocorax serdicensis Burchak-Abramovic & Nikolov, 1984	Late Miocene (MN11–13)	Bulgaria
Phalacrocorax longipes (Tugarinov, 1940)	Late Miocene (MN11–13), Early Pliocene (MN15)	Ukraine
Nectornis miocaenus (Milne-Edwards, 1867)	Early Miocene (MN2–4)	France, Germany, Czechia
Nectornis anatolicus (Mourer-Chauviré, in Paicheler *et al*., 1978)	Miocene	Turkey
?*Limicorallus carbunculus* (Mayr, 2009)	Early Miocene	Germany

Oligocorax littoralis, P. intermedius, and *N. miocaenus* were originally described in the genus *Graculus* Koch, 1816, and were later referred to *Phalacrocorax*. The species *miocaenus* was moved to *Nectornis* by Cheneval (1984), while the species *littoralis* was only recently returned to the genus *Oligocorax* by Mayr (2001).

Here we describe a new species from the Lower Miocene of Rauscheröd, southern Germany.

Geology and stratigraphy of the locality. The locality of Rauscheröd, near Ortenburg, southwest of Passau, is situated in the North Alpine Foreland Basin, southeastern Germany (Lower Bavaria) (Fig. 1). The deposits at Rauscheröd represent the transition of brackish sediments of the Brackwater Molasse (Ottnangian) to the overlying limno-fluviatile sediments of the Upper Freshwater Molasse (Karpatian–Sarmatian). The bird bones come from the more brackish sediments outcropping in the basal part of the Rauscheröd gravel pit section. These sediments belong to the so-called "Ortenburger Schotter" (late Ottnangian–early Karpatian) (see Grimm, 1977; Lang, 2009), which are mostly interpreted as delta deposits (Schlickum & Strauch, 1968; Haas, 1987; Lang, 2009) that were discharged in the eastern part of the western Paratethys. The "Ortenburger Schotter" is composed of basal, fine-grained and brackish bottom-sets, overlaid by thick strata of coarse gravels and sands representing the delta fore-sets and topped by fine, limnic sediments of the top-sets, and can reach 20 to 40 m thickness (Lang, 2009). The "Ortenburger Schotter" is overlaid in the Rauscheröd gravel pit by an 18 m thick deposit of clays and marls (lacustrine sediments) of the limno-fluviatile Upper Freshwater Molasse (Ziegler & Fahlbusch, 1986).

The vertebrate fauna of Rauscheröd is dominated by micromammals, based on which Ziegler & Fahlbusch (1986) referred it to the Mammalian Neogene Unit MN4b (Karpatian, Early Miocene). Large terrestrial mammals are represented by rhinoceroses (*Prosantorhinus* cf. *Pr. douvillei, Brachypotherium brachypus, Alicornops simorrensis* [pers. comm. K. Heissig, Munich]), proboscideans (*Gomphotherium, Prodeinotherium*) and cervids (*Procervulus dichotomus* [see Rössner, 1995]). The aquatic fauna is made up by freshwater elements, like beavers, crocodiles, turtles and fishes (perches), as well as marine vertebrates like sirenians (which might have been able also to live in brackish water) and sharks (Odontaspididae) (see Pfeil & Werner, 1991). In the middle part of the "Ortenburger Schotter", silicified wood (e.g., palm-trees) of great size (up to some meters) can be found (Selmeier, 1983; Ziegler & Fahlbusch, 1986). By means of the flora, especially the silicified wood fossils, Selmeier (1983) reconstructed a tropical to subtropical coastal forest along the eastern shores of the western Paratethys.

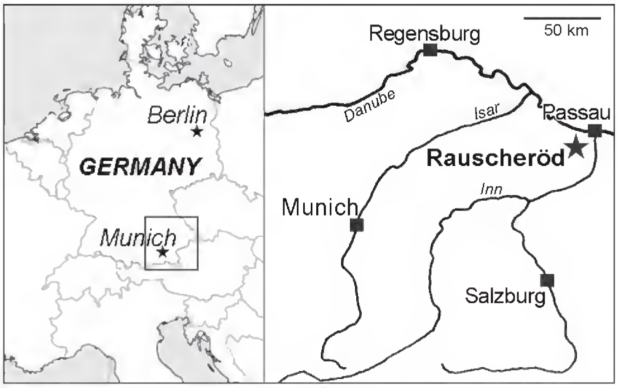

Figure 1. Geographical position of the locality Rauscheröd (southeastern Germany, Lower Bavaria).

Material and methods

The presented material is housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich (Inventory number BSPG 1990 VI, collection R. Baumgartner).

The osteological terminology follows Baumel & Witmer (1993) and occasionally Ballmann (1969); measurements were taken after von den Driesch (1976).

Abbreviations: Collections: *BSPG*, Bayerische Staatssammlung für Paläontologie und Geologie, Munich; *MNHN*, Muséum national d'Histoire naturelle, Paris; *NHMW*, Naturhistorisches Museum Wien; *UCBL*, Université Claude Bernard-Lyon 1. Other abbreviations: *cmc*, carpometacarpus; *cor*., coracoid; *dist*., distal; *hum*., humerus; *L*, left; *mc*, metacarpal; *MN*, Mammal Neogene unit; *MP*, Mammal Paleogene unit; *prox*., proximal; *R*, right; *rad*., radius; *scap*., scapula; *tbt*, tibiotarsus; *tmt*, tarsometatarsus.

All of the extinct taxa of Phalacrocoracoidea cited above, as well as a selection of extant ones, have been considered for osteological comparisons with the fossils presented here.

The following taxa have been studied first hand: Fossil species: *O. littoralis* (MNHN, UCBL), *N. miocaenus* (MNHN, UCBL), *P. serdicensis* (casts at UCBL). Extant species: *P. carbo, P. aristotelis, P. (Microcarbo) melanoleucos, A. anhinga* (UCBL, NHMW).

Systematic paleontology

Order Pelecaniformes Sharpe, 1891

Phalacrocoracoidea *sensu* Livezey & Zusi, 2007

Borvocarbo Mourer-Chauviré, Berthet & Hugueney, 2004

Type species. *Borvocarbo guilloti* Mourer-Chauviré, Berthet & Hugueney, 2004, represented only by a coracoid from Créchy (Allier, France), Late Oligocene (MP30).

Additional species. ?*Borvocarbo stoeffelensis* Mayr, 2007, dissociated skeleton from Enspel (Germany), Late Oligocene (MP28).

?*Borvocarbo tardatus* n.sp.

Figs 2, 3

Holotype. Nearly complete left tibiotarsus (BSPG 1990 IV 16), figured also in Pfeil & Werner, 1991, pl. 5, fig. 2.

Paratypes. Proximal half of left ulna (BSPG 1990 IV 17), proximal third of right radius (BSPG 1990 IV 18).

Type locality. Gravel pit of the company "Sand- und Kieswerk Rauscheröd Ulrich Alex GmbH" in the village of Rauscheröd, near Passau (eastern Lower Bavaria, southeastern Germany), (topographic map 7445 Ortenburg, r: 4592970 h: 5380700). Early Miocene, MN4b, transition of upper Brackish Molasse to Upper Freshwater Molasse.

Etymology. From the Latin *tardatus*, meaning late; used in the sense that this species is the stratigraphically youngest (latest) of the genus *Borvocarbo* and that it retained primitive osteological characters up to the Early Miocene. All contemporaneous cormorant taxa show more derived osteological features.

Diagnosis. Largest species of *Borvocarbo*. Size between that of the extant cormorants *P. carbo* and *P. aristotelis*. Ulna with processus cotylaris dorsalis lacking hook-like distal end. Tibiotarsus with sulcus extensorius in almost central position along midline, with pons supratendineus proximodistally wide and almost horizontal, and condylus medialis extending only slightly further distally than condylus lateralis. These morphological characters also characterize ?*B. stoeffelensis*, but ?*B. tardatus* is distinctly larger.

Description

The left tibiotarsus (Fig. 2) is nearly complete, with only the cranial and proximal part of the crista cnemialis cranialis and the proximal ends of the crista patellaris and crista cnemialis lateralis broken off. However on the cranial face, in proximal view, the remaining part of the crista patellaris is roughly aligned mediolaterally and this indicates that the tip of the crista cnemialis lateralis was not offset cranially. In proximal view, the incisura tibialis is deeply marked. Two strong and projecting tubercles are situated on the proximal end, a smaller one on the area interarticularis and a larger one caudal to the facies articularis lateralis. In proximal view, the lateral margin of the facies articularis lateralis is somewhat flattened. The crista fibularis is strong and about 26 mm long. The shaft is oval in cross section and slightly compressed craniocaudally. The distal end is distinctly medially bent. The canalis extensorius is wide and runs obliquely from distomedially to proximolaterally and the sulcus extensorius extends along the midline of the shaft. Situated lateral to the pons supratendineus, the tuberositas retinaculi extensoris is developed as a moderate tuberculum, which is separated from the condylus lateralis by a weak sulcus. The tuberculum retinaculi m. fibularis is long and its proximal end merges smoothly into the shaft. Condyli medialis and lateralis are of almost equal size and are parallel and oriented vertically (in cranial view). The condylus medialis bears a deep indentation on its lateral side. The condylus medialis is only slightly longer in distal direction than the condylus lateralis and also exceeds the latter in craniocaudal direction. In distal view, the condylus medialis is tilted craniolaterally so that the distal trochlea tapers from the cranial end to the caudal one. For measurements, see Table 2.

Only the proximal half of the left ulna (Fig. 3) is preserved. The cotyla dorsalis is slightly narrower than the cotyla ventralis. The dorsal projection of the cotyla dorsalis (processus cotylaris dorsalis) is blade-like and does not form a distal hook. The olecranon is swollen proximally and caudally and projects ventrally. The impressio m.

Table 2. Measurements (in mm) of the tibiotarsus and ulna of ?*B. tardatus* and other available Tertiary taxa of phalacrocoracoids for comparison. *GL*, greatest length (including processus cnemialis); *L*, length (without processus cnemialis); *dWp*, proximal diagonal width; *WD*, smallest width of shaft; *Wd*, distal width; *Wp*, proximal width; *Dd*, distal depth; *Dp*, proximal depth; *Dgd*, largest diagonal distal. Asterisk * indicates type localities. Estimated measurements of slightly worn bones are given in parentheses.

tibiotarsus		GL	L	dWp	WD	Wd	Dd
?*Borvocarbo tardatus* n.sp.	*Rauscheröd (D)	ca. 112	107.1	20.1	7.3	13.7	12.5
?*Borvocarbo stoeffelensis*	*Enspel (D)	81.3	—	—	—	—	—
Oligocorax littoralis	*St-Gérand-le-Puy (F)	—	—	—	5.4	9.6–9.9	—
Nectornis miocaenus	*St-Gérand-le-Puy (F)	73	69.1	(12)	4.8	8.3	8.6

ulna		GL	Dp	Wp	WD	Dd	Dgd
?*Borvocarbo tardatus* n.sp.	*Rauscheröd (D)	—	16	13.5	7	—	—
?*Borvocarbo stoeffelensis*	*Enspel (D)	ca. 108	—	—	—	—	—
Oligocorax littoralis	*St-Gérand-le-Puy (F)	—	—	9.2	4.2	—	—
Nectornis miocaenus	*St-Gérand-le-Puy (F)	89.5–102	10–11	8–9	3.3–4.4	5.5–7.2	6.4–6.6

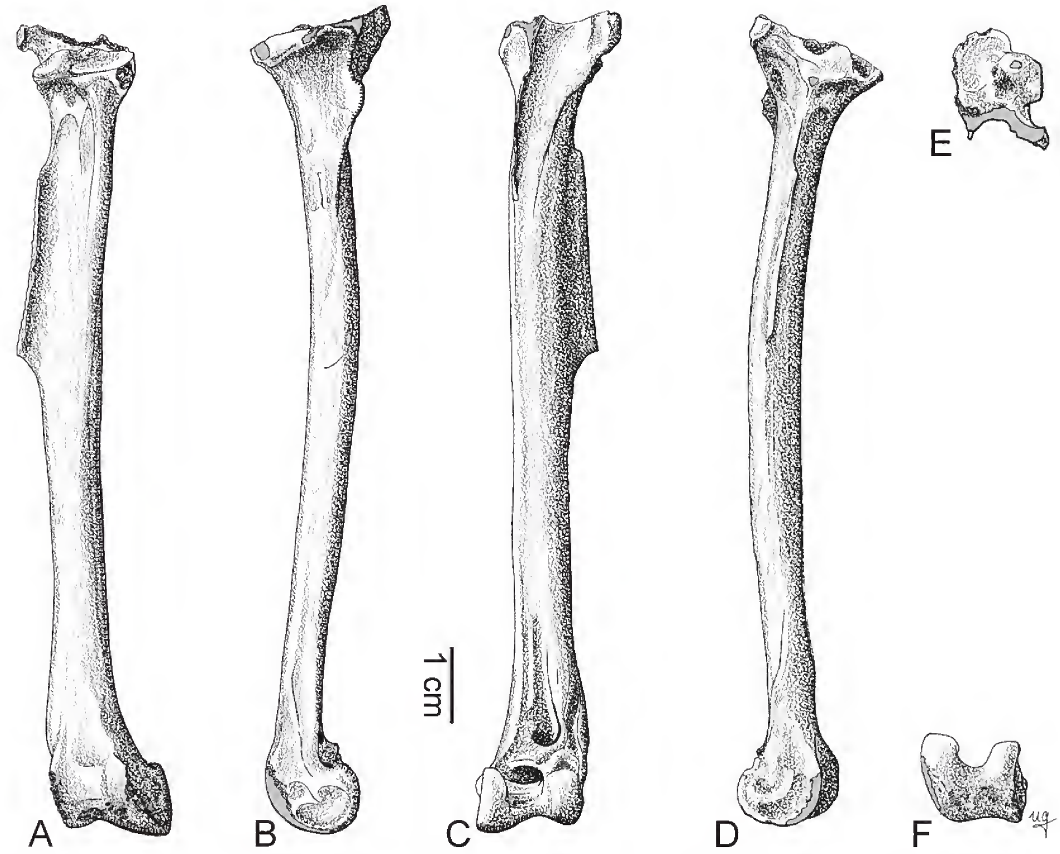

Figure 2. ?*Borvocarbo tardatus* n.sp. from the Early Miocene of Rauscheröd, left tibiotarsus (BSPG 1990 IV 16, holotype) in (*A*) caudal, (*B*) medial, (*C*) cranial, (*D*) lateral and (*E*) proximal, (*F*) distal aspects. Grey-shaded areas indicate damages.

scapulotricipitis on the dorsal side of the proximal end forms a small but distinctive pit; the impressio m. brachialis is well marked, about 3 cm long and becomes shallow distally. The insertion for the lig. collateralis ventralis on the ventral side of the proximal end is large and flat. The linea intermuscularis along the median cranial surface of the proximal shaft forms a prominent crest. The quill knobs (papillae remigales caudales) are weakly developed.

Only the proximal third of a right radius (Fig. 3) is preserved. The ventral margin of the cotyla humeralis is broken off. The caput radii on the proximal end is dorsally strongly swollen. The tuberculum bicipitale radii, situated ventrally somewhat distally to the proximal end, forms a short crest-like structure. The linea intermuscularis ventralis becomes more prominent distally.

Comparisons. Most of the Miocene cormorant taxa are created on, and are represented by, only scanty material, often a single bone, which makes comparisons, systematic determinations and phylogenetic discussions with these taxa difficult. For only a few species are a tibiotarsus, ulna and/or radius available for metrical and morphological comparisons (Table 3) with the material from Rauscheröd described here.

For comparison with extant taxa we consulted the only two European taxa, the Great Cormorant (*Phalacrocorax carbo*) and the European Shag (*P. aristotelis*, genus "*Stictocarbo*" after Siegel-Causey, 1988), and a representative of the microcormorants and the darters. The last are usually accepted to be a sister taxon of cormorants; for our comparisons, we selected an American Darter (*Anhinga anhinga*, North to South America).

The relationship of microcormorants (genus *Microcarbo* after Siegel-Causey, 1988) and other Phalacrocoracidae is still controversial. The osteological investigations of Siegel-Causey (1988) resulted in a position of the *Microcarbo* species within the taxon "Phalacrocoracinae" ("cormorants"), which itself is considered as a sister taxon of "Leucocarboninae" (shags). On the other hand, the analyses of mitochondrial sequence data by Kennedy *et al.* (2000) found that the microcormorants are the sister group of all other Phalacrocoracidae. Owing to the probable basal phylogenetic position of the microcormorants, we considered also the Little Pied Cormorant (*P. (M.) melanoleucos*, Australia, New Zealand, Tasmania, Indonesia, and some adjacent islands) for comparisons (hereafter *Microcarbo melanoleucos*).

Numbers in the following descriptions refer to features in Figs 4 and 5.

Comparison of tibiotarsus (Fig. 4). In comparison with the tibiotarsi of the extant taxa *Phalacrocorax carbo* and *P. aristotelis*, that of ?*B. tardatus* differs by having (1) higher and stronger protuberances proximal on the facies articularis. (2) thickening at the tip of the crista cnemialis lateralis, slightly more developed than in *Anhinga* and in ?*B. stoeffelensis* (Mayr, 2007, fig. 6G), but less developed than in *Microcarbo*. Crista patellaris roughly aligned mediolaterally indicating that the tip of the crista cnemialis

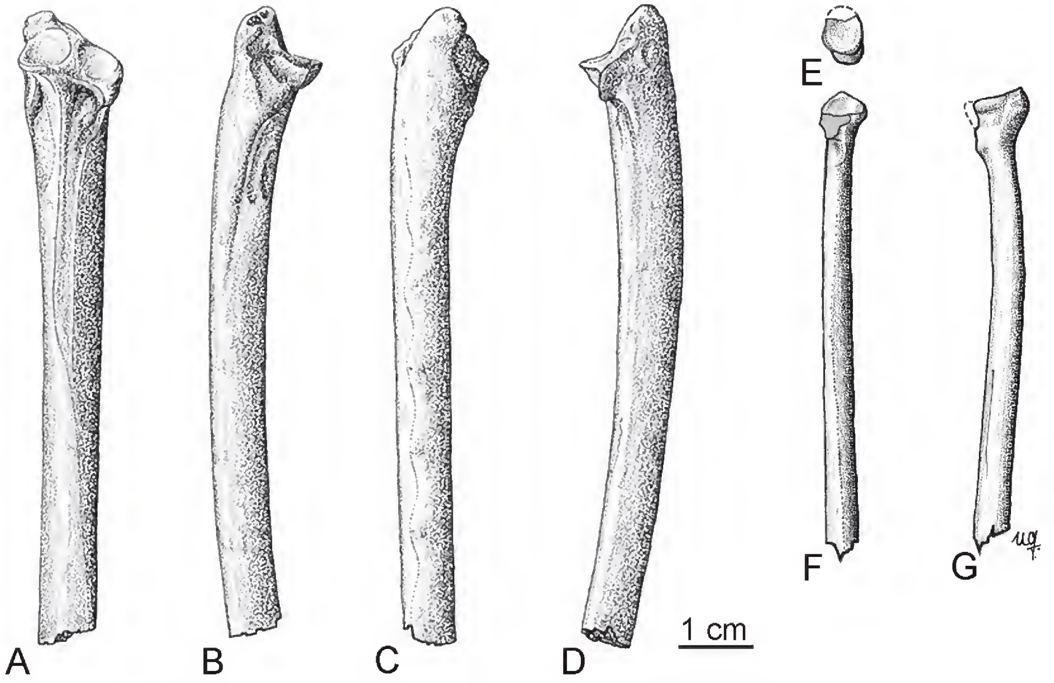

Figure 3. ?*Borvocarbo tardatus* n.sp. from the Early Miocene of Rauscheröd, left ulna (BSPG 1990 IV 17, paratype) in (*A*) cranial, (*B*) ventral, (*C*) caudal and (*D*) dorsal aspects, and right radius (BSPG 1990 IV 18, paratype) in (*E*) proximal, (*F*) ventral and (*G*) caudal aspects. Grey-shaded areas indicate damages.

Table 3. Availability of comparative material of fossil Oligocene and Miocene taxa of Phalacrocoracoidea from Europe and circum-Mediterranean regions.

fossil taxon	occurrence	tbt	prox. ulna	prox. radius	elements
Phalacrocorax					
P. intermedius	France, Germany, Austria, early Middle Miocene	—	—	—	humerus, coracoid, prox.cmc, vertebra
P. ibericus	Valles de Fuentiduena (Spain), Upper Miocene (MN9)	—	—	—	dist.humerus
P. lautus	Golboçica (Moldova), Upper Miocene (MN9?)	—	—	—	prox.femur, dist.ulna
P. serdicensis	Hrabarsko (Bulgaria), Late Miocene (MN11–13)	—	—	●	prox.humerus, prox.+dist. cmc, cran.+caud.coracoid, sternum, prox. scapula, prox.radius, dist.ulna
P. longipes	Ukraine, Late Miocene and Pliocene	—	—	—	prox.femur
Borvocarbo					
B. guilloti	Créchy, Allier (France), Late Oligocene, MP30	—	—	—	coracoid
?*B. stoeffelensis*	Enspel (Germany), Oligocene	●	●	●	partial skeleton
Oligocorax					
O. littoralis	France, Early Miocene	●	●	—	humerus, prox.ulna, femur, dist.tbt, prox.tmt
Nectornis					
N. miocaenus	France, Germany and Czechia, Lower Miocene	●	●	●	coracoid, scapula, ulna, radius, cmc, femur, tbt, tmt, sternum, furcula, pelvis
N. anatolicus	Turkey, Early/Middle Miocene	—	—	—	coracoid, prox.humerus, dist.ulna, dist.radius, cmc
Limicorallus					
?*L. carbunculus*	Probably Mainz-Weisenau (Germany), Lower Miocene	—	—	—	tmt
Anhinga					
A. pannonica	Tatarus-Brusturi (Romania) and Götzendorf (Austria), Late Miocene; Tunisia, Late Miocene	—	—	—	vertebra, humerus

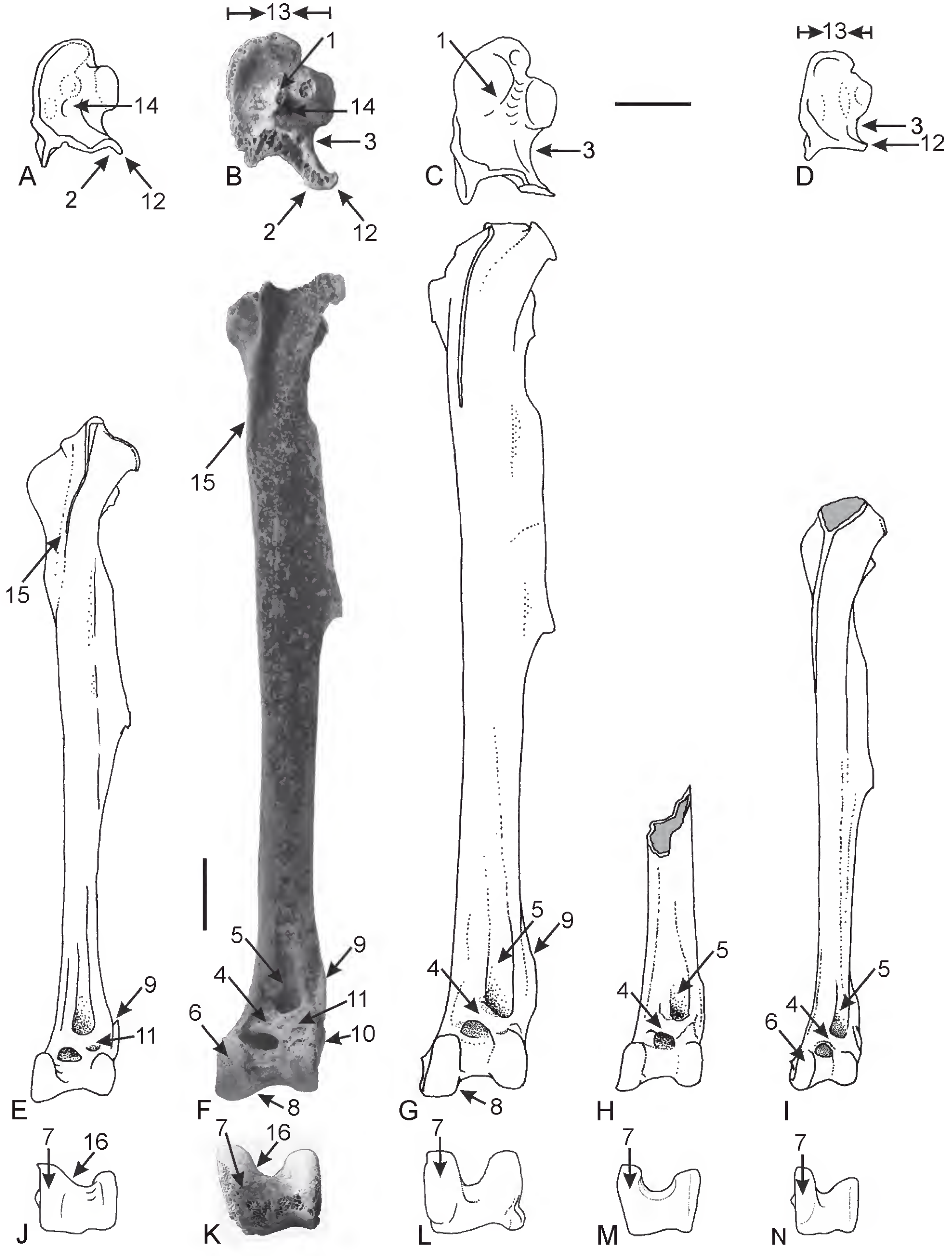

Figure 4. Distinguishing features of the tibiotarsi of (*A, E, J*) *Anhinga anhinga*, (*B, F, K*) ?*Borvocarbo tardatus* n.sp., (*C, G, L*) *Phalacrocorax carbo*, (*H, M*) *Oligocorax littoralis* (inverse, MNHN Av 9432), and (*D, I, N*) *Nectornis miocaenus* (MNHN Av 9411); in proximal (A–D), cranial (E–I), and distal (J–N) aspects.

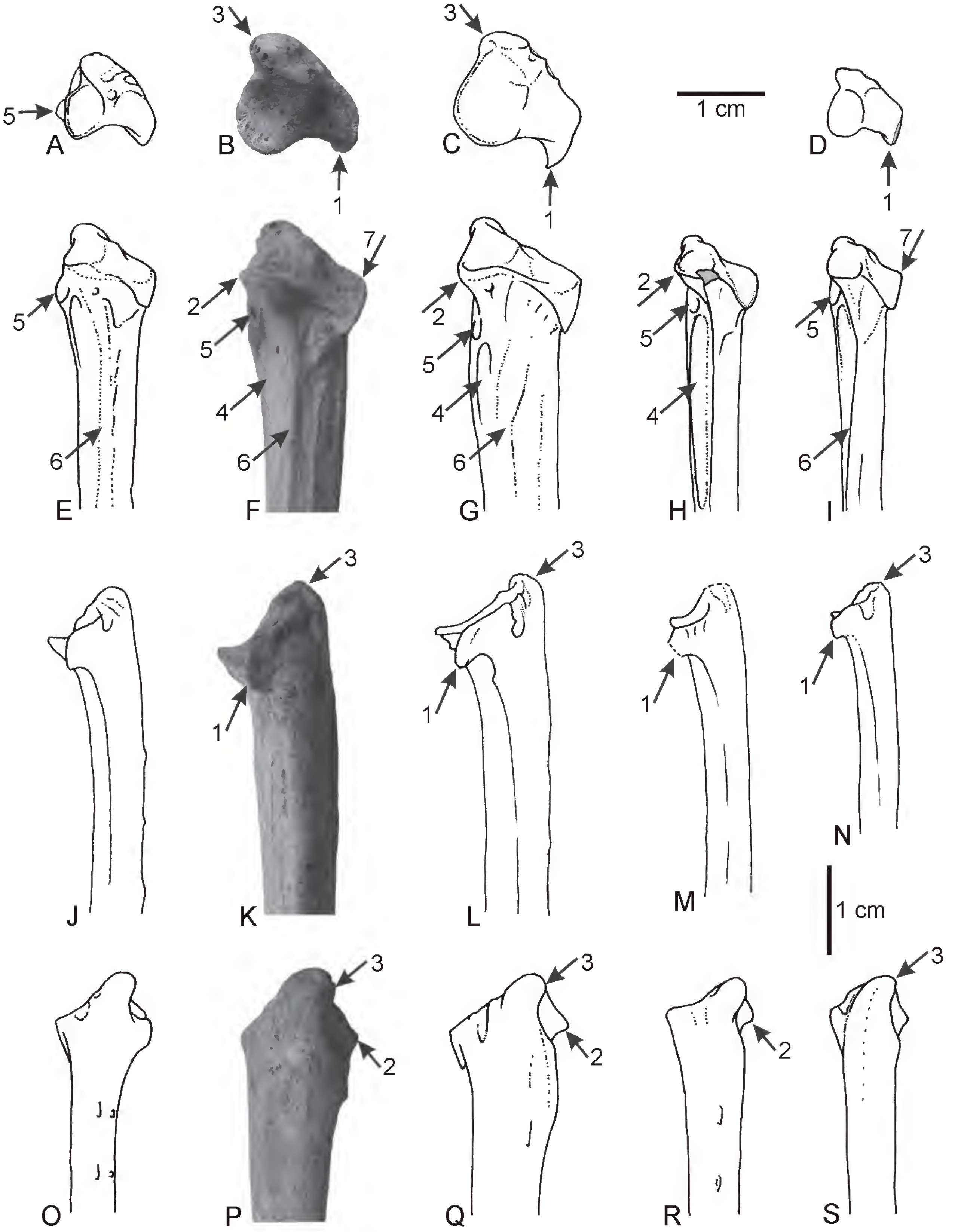

Figure 5. Distinguishing features of the ulnae of (*A, E, J, O*) *Anhinga anhinga*, (*B, F, K, P*) ?*Borvocarbo tardatus* n.sp., (*C, G, L, Q*) *Phalacrocorax carbo*, (*H, M, R*) *Oligocorax littoralis* (MNHN Av 9430) and (*D, I, N, S*) *Nectornis miocaenus* (MNHN Av 9375); in proximal (*A–D*), cranial (*E–I*), dorsal (*J–N*) and caudal (*O–S*) aspects.

lateralis was not offset cranially. (3) incisura tibialis deeply expressed, as for example in *Anhinga*, while in *P. carbo, P. aristotelis* and *Microcarbo* it makes a shallow curve. (4) a less oblique (almost horizontal) and proximodistally wide pons supratendineus and (5) a sulcus extensorius that runs almost in the midline of the shaft (more laterally in *Phalacrocorax*, meaning in *P. carbo* and *P. aristotelis* also in the following text). (6) The condylus medialis is stronger (about same size as condylus lateralis) than in *Phalacrocorax* and, in distal view, (7) is tilted slightly obliquely in the mediocranial direction so that the distal trochlea tapers slightly caudally, whereas in *Phalacrocorax* the condyles and their medial and lateral margins are almost parallel. In cranial view, (8) the condylus medialis is distally shorter than in *Phalacrocorax*, only slightly distally surpassing the lateral one. (9) The tuberculum retinaculi m. fibularis is less prominent and proximally ends less abruptly than in extant *Phalacrocorax*. (10) The epicondyli medialis and lateralis are stronger than in extant *Phalacrocorax*. (9) The apophysis externa ligamenti obliqui (Ballmann, 1969) is stronger and more individualised.

The microcormorant *Microcarbo melanoleucos* is almost half of the size of ?*B. tardatus* and furthermore differs in its tibiotarsus in the aforementioned mentioned features (3) (4), (5), (6), (7), (10), and (11). In *M. melanoleucos*, (2) the crista patellaris is roughly flat and aligned lateromedially and joins the caudal side of the thickened tip of the crista cnemialis lateralis, (4) the pons supratendineus is more oblique, (5) the sulcus extensorius runs more laterally, (6) the condylus medialis is more slender (in cranial and distal views) than the lateral one and, in cranial view, is tilted distomedially (almost vertical in ?*B. tardatus*), and (10) the epicondyli medialis and lateralis and (11) the apophysis externa ligamenti obliqui are weaker. Furthermore, in proximal view, the lateral prominence for the contact with the caput fibulae is more pointed in *M. melanoleucos*.

No tibiotarsus of *P. intermedius* is known so far. Metrical comparisons of other skeletal elements suggest that *P. intermedius* and ?*B. tardatus* might have been of similar size. On the other hand, *N. miocaenus, N. anatolicus* and *O. littoralis* are all distinctly smaller than the new Rauscheröd cormorant.

Unlike the tibiotarsus of *O. littoralis* from Saint-Gérand-le-Puy (MN2, France) (Milne-Edwards 1867–1871b, pl. 42, figs 9–12) that of ?*B. tardatus* differs by the aforementioned features (4) and (5): (4) the pons supratendineus is less oblique in transversal direction in comparison to that of *O. littoralis*. In distal view, (7) the distal condyles of both taxa are similar in tapering slightly caudally, but in *P. littoralis*, the condyles are oriented more parallel, whereas in ?*B. tardatus* the condylus medialis is slightly oblique.

The tibiotarsus of ?*B. tardatus* differs from that of *Nectornis* by its more cranially projecting crista cnemialis cranialis (in medial view) and by (12) a much more projecting and craniolaterally oriented crista cnemialis lateralis (in proximal view). (13) The proximal end is mediolaterally wider (in relation to depth) and the lateral margin of the facies articularis lateralis projects more laterally. (5) The sulcus extensorius runs almost along the midline of the shaft (situated more laterally in *Nectornis*) and (4) the pons supratendineus is less oblique in transversal and cranial directions than in *Nectornis*. (6) The condylus medialis is broader and (7) tapers slightly caudally (in distal view) in ?*B. tardatus*, whereas the medial and lateral margins are parallel in *Nectornis*.

In contrast to the conditions in *A. anhinga*, in ?*B. tardatus* (14) the fossa synovialis externa (Ballmann, 1969) on the proximal end of the tibiotarsus is deeper and (12) the crista cnemialis lateralis projects further craniolaterally (in proximal view). (15) The crista cnemialis cranialis is cranially convex at its distal base (in medial view) (concave in *Anhinga*). (9) The tuberculum retinaculi m. fibularis is situated more proximally on the distal end and (11) the apophysis externa ligamenti obliqui forms a strong tubercle proximal to the condylus lateralis, whereas in *A. anhinga* it forms a deep fossa. In distal view, (16) the incisura intercondylaris in ?*B. tardatus* is less asymmetric. ?*B. tardatus* and *A. anhinga* agree well in the presence of strong protuberances on the proximal articular surface, the shape of the incisura tibialis, the position of the sulcus extensorius and the orientation of the pons supratendineus.

As in ?*B. stoeffelensis*, the condylus medialis of the distal tibiotarsus of ?*B. tardatus* protrudes only slightly further distally than the condylus lateralis (Mayr 2007). Unfortunately, the second diagnostic feature of the tibiotarsus of ?*B. stoeffelensis*, the crista patellaris without lateral proximal projection, cannot be ascertained because of the incomplete preservation of the Rauscheröd tibiotarsus.

Comparison of ulna (Fig. 5). The proximal ulna of ?*B. tardatus* is distinguished from those *P. carbo* and *P. aristotelis* by having (1) a less prominent and less projecting processus cotylaris dorsalis without a hook-like distal end; (2) the ventral edge of the cotyla ventralis projecting less ventrally; (3) the olecranon more swollen and projecting more proximally (best observed in caudal view, difference in elevation between proximal end of cotyla ventralis and of olecranon); (4) the impressio brachialis shallower proximally; (5) the tuberculum lig. collateralis ventralis situated more proximally, just below the margin of the cotyla ventralis (more distally in *P. carbo* and *P. aristotelis*); (6) the linea intermuscularis forming a more prominent crest along the midline of the cranial surface of the proximal shaft.

Several of these aforementioned distinguishing features between the ulna of ?*B. tardatus* and those *P. carbo* and *P. aristotelis* do not distinguish between ?*B. tardatus* and the microcormorant *M. melanoleucos*. However, beside the distinctly smaller size of the *M. melanoleucos*, the species also clearly differs from ?*B. tardatus* by having (1) a well-developed hook-like projecting processus cotylaris, (3) a less swollen and less proximoventrally projecting olecranon, and a less cranially projecting margin of the cotyla ventralis.

Unlike in *O. littoralis* (Milne-Edwards, 1867–1871b, pl. 44, figs 6–8), in ?*B. tardatus* (1) the processus cotylaris dorsalis is less prominent and less projecting, without a hook-like distal end (even if a little broken in *O. littoralis*); (5) the tuberculum lig. collateralis ventralis is situated more proximally; (2) the ventral edge of the cotyla ventralis projects less ventrally, and (4) the impressio brachialis is shallower (also in its distal extent).

In contrast to that of *N. miocaenus*, the ulna of ?*B. tardatus* has (1) the processus cotylaris dorsalis without the hook-like distal end, (3) the olecranon more swollen and projecting slightly more proximally, (5) the tuberculum lig. collateralis ventralis projecting slightly less ventrally, (7) the dorsocaudal border of the cotyla dorsalis rounded (in *Nectornis* it forms an angle) and (6) the crest-like linea intermuscularis along the proximal part of the cranial surface of the shaft more prominent than in *Nectornis*.

Unlike that of *A. anhinga*, the tuberculum lig. collateralis ventralis of ?*B. tardatus* is (5) weaker and less projecting ventrally and (6) the crest-like linea intermuscularis is more prominent.

Unlike in members of the compared fossil and extant Phalacrocoracidae (inclusive also *M. melanoleucos*), but similar to *Borvocarbo*, species of the Anhingidae have the distal hook-like process of the cotyla dorsalis less developed.

Comparison of radius. The proximal end of the radius of ?*B. tardatus* is more similar to that of *Anhinga* than to those of extant cormorants, in which the tubercle-like caput radii is more prominent and projects further dorsally than in the Rauscheröd specimen.

Discussion and results

The detailed osteological comparisons above exclude an affiliation of the present material to the taxa *Phalacrocorax* (represented by *P. carbo* and *P. aristotelis*), the microcormorants (represented by *M. melanoleucos*), *Nectornis*, and *Oligocorax*. Furthermore, ?*L. carbunculus* differs from the Rauscheröd form by its diminutive size. Even if there are some morphological resemblances to *Anhinga*, the cormorant from Rauscheröd shows best correspondence with *Borvocarbo*.

The original description and diagnosis of the genus *Borvocarbo* (Mourer-Chauviré *et al.*, 2004) is based on only a coracoid of *B. guilloti* from the Late Oligocene of Créchy (France). Recently, Mayr (2007) described the new cormorant species ?*B. stoeffelensis*, based on a partial skeleton from the Late Oligocene of Enspel (Germany), which he tentatively referred to *Borvocarbo*. A definite generic assignment was not possible because the type species was itself described from only a coracoid, which in the Enspel fossil is very poorly preserved.

In the case of the Rauscheröd cormorant material, the coracoid is also unknown, but the ulna and tibiotarsus share some characteristic features with ?*B. stoeffelensis*. Another reason to assign the Rauscheröd form to ?*Borvocarbo* is its possession of primitive osteological characters compared to those of the Neogene forms.

The new species ?*B. tardatus* from Rauscheröd is distinctly larger than both ?*B. stoeffelensis* and *B. guilloti* and is thus the largest representative of *Borvocarbo*. The estimated size of ?*B. tardatus* is between the *P. carbo* and *P. aristotelis*; the greatest length of the tibiotarsus is about 27% longer than that of ?*B. stoeffelensis*. According to Mayr (2007), the absences of a hook-like distal projection of the processus cotylaris dorsalis on the ulna and of a proximal process on the crista cnemialis lateralis on the proximal tibiotarsus are plesiomorphic features within Phalacrocoracoidea (Mayr, 2007). Unfortunately, the latter character is not preserved in the ?*B. tardatus* material. Mayr (2007) concluded that ?*B stoeffelensis* is positioned outside the crown group Phalacrocoracidae + Anhingidae. All the characters described here for the tibiotarsus, ulna, and radius of ?*B. tardatus* are plesiomorphic in comparison with the Recent Phalacrocoracidae.

If the attribution to the genus *Borvocarbo* were to be correct, this new record extends the stratigraphical range of *Borvocarbo* from the Late Oligocene into the Early Miocene of Europe.

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A New Eagle (Aves: Accipitridae) from the Mid Miocene Bullock Creek Fauna of Northern Australia

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ABSTRACT. A large accipitrine bird of prey is described from the Mid Miocene Camfield Beds, Bullock Creek, Northern Territory, Australia, based on a distal humeral fragment. Comparisons with the larger living Australian eagles show that this bird belongs in *Aquila* rather than *Haliaeetus*. It can be differentiated from living species of *Aquila* by morphology and size, and is here named as a new fossil species. This specimen comprises the oldest record of this genus in Australia, and possibly the oldest in the world.

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The Accipitridae has a relatively rich fossil history worldwide. In Australia, named fossil taxa are restricted to *Pengana robertbolesi* from the Early Miocene (Boles, 1993) and several species described from the Quaternary by C.W. de Vis (1890, 1891, 1892, 1905). Other accipitrids are known (Vickers-Rich, 1991) but await detailed examination. This paper describes a new eagle species from the Accipitridae from the Camfield Beds, Bullock Creek, Northern Territory (Fig. 1). It is part of the Bullock Creek Fauna. These deposits are considered to be Mid Miocene in age (Murray & Megirian, 1992).

Methods

Anatomical nomenclature follows Baumel & Witmer (1993) and Owre (1967) for identification of muscles insertions on the distal end of the humerus. Measurements follow the methods illustrated by von den Driesch (1976) and were made with vernier calipers accurate to 0.05 mm and rounded to the nearest 0.1 mm. The fossil is lodged in the Queen Victoria Museum and Art Gallery, Launceston, Tasmania (QVM); comparative material was examined at, or borrowed from, Museum Victoria, Melbourne, Australian Museum, Sydney; and Australian National Wildlife Collection, Canberra. Higher level taxonomy of the Accipitridae follows Lerner & Mindell (2005).

Comparative material

The Bullock Creek accipitrid is a large-bodied animal, exceeding in size all extant Australian taxa except those in the genera *Aquila* and *Haliaeetus*. Comparisons of the specimen were made with Australian and extralimital species of these genera and of *Hieraaetus*, sister genus to *Aquila* and also represented in Australia. Lerner & Mindell (2005) and Helbig *et al.* (2005) found that *Aquila* and *Hieraaetus*, as conventionally circumscribed, were polyphyletic relative to each other. Some authors (e.g., Sangster *et al.*, 2005) synonymized the two genera. Louchart *et al.* (2005) found it

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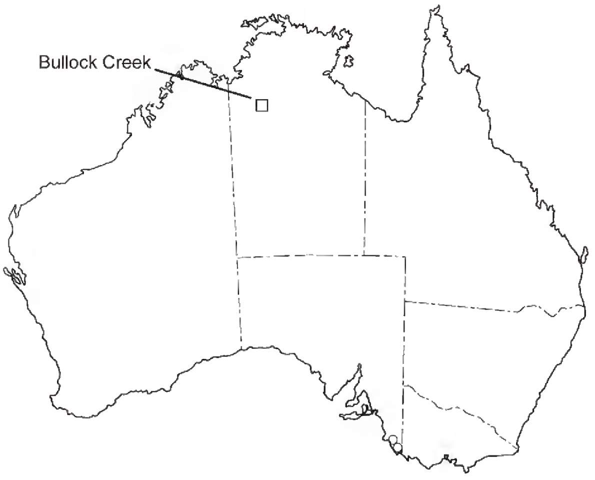

Figure 1. Location of Bullock Creek, Northern Territory, type location of *Aquila bullockensis*.

difficult to separate members of these genera osteologically. Although it is likely that they will be combined, here they are kept separate for ease of reference in the text. The only species examined in this study that is affected by this change is *Hieraaetus fasciatus*, which becomes *Aquila fasciata*. Although living species of *Hieraaetus* are considerably smaller than the fossil, it was shown by Bunce *et al.* (2005) that the recently extinct New Zealand *"Harpagornis" moorei*, considerably larger than any extant species of accipitrid, should be placed in *Hieraaetus*.

Although no detailed evidence has been presented, the suggestion has been made that among the undescribed birds of prey are Old World vultures (Rich & van Tets, 1982; van Tets & Rich, 1990). This title applies to two non-sister clades of accipitrids, Gypaetinae and Aegypiinae, neither of which occurs in Australia today. Owing to this previous suggestion, representatives of both were included in the comparisons, as was the Osprey (*Pandion haliaetus*: Pandionidae), sister taxon of the Accipitridae.

The following species were used for comparison in this study: (Aegypiinae) *Necrosyrtes monachus, Gyps fulvus, G. coprotheres, Sarcogyps calvus, Aegypius monachus*, (Gypaetinae) *Neophron percnopterus*, (Aquilinae) *Aquila audax, A. chrysaetos, A. fasciata, Hieraaetus morphnoides, H. pennatus* and (Haliaeetinae) *Haliaeetus leucogaster, H. albicilla* and *H. leucocephalus*, Pandionidae (*Pandion haliaetus*).

Systematic paleontology

Family Accipitridae (Vigors, 1824)

The Bullock Creek humerus can be distinguished from that of both groups of Old World vultures because it possesses a shallower fossa m. brachialis, more bulbous processus flexorius and a relatively broader condylus dorsalis. *Pandion* differs by its reduced epicondylus dorsalis, more excavated fossa m. brachialis, narrower fossa olecrani and narrower condyles. The two species of *Hieraaetus* examined show almost no differences from species of *Aquila*. Other than a somewhat more pronounced gap between the processus flexorius and condylus ventralis (in distal view), the only significant character is one of size (see also Louchart *et al.*, 2005).

Species of *Aquila* (based on *A. audax, A. chrysaetos* and *A. fasciata*) and *Hieraaetus* (*H. morphnoides* and *H. pennatus*) can be distinguished from those of *Haliaeetus* (*H. leucogaster, H. leucocephalus*) by the same suite of distal humeral characters (Fig. 2): (1) the ventral side of the distal end, including the epicondylus ventralis, projects further ventrally, in cranial view, (2) the fossa olecrani is shallower (deeper, more defined in *Haliaeetus*); (3) the scar for M. pronator superficialis (proximal to the tuberculum supracondylare ventrale) is deeper and more circular (slightly shallower, less defined circle); (4) the incisura intercondylaris is excavated distally, in cranial view (not visible in specimen of *A. fasciata*) (not excavated); (5) the processus flexorius is round and protruding distally in cranial view and caudally in medial view (base less rounded, not projecting as far distally or medially); (6) the tuberculum supracondylare ventrale is attenuated proximodorsally (rounded dorsally); and (7) the ratio of shaft width to distal width is less (greater) (Table 1; Fig. 3).

The Bullock Creek humerus agrees with those of extant species of *Aquila* in all these character states. It more closely resembles these species than those of *Hieraaetus morphnoides* and *H. pennatus* by having a reduced gap between the processus flexorius and condylus ventralis. Accordingly, the fossil is assigned to *Aquila*.

Genus *Aquila* Linnaeus, 1758

The Bullock Creek taxon can be distinguished from the extant species *A. audax, A. chrysaetos* and *A. fasciata* on differences in size and morphology applicable to all three. It is therefore assigned to a new species.

Aquila bullockensis n.sp.

Fig. 4

Holotype. distal end of right humerus, QVM:2000:GFV:154.

Locality and stratigraphy. Bin 23, Bullock Creek (Fig. 1); Camfield Beds.

Age. Mid-Miocene, 11–5mya.

Etymology. Bullock Creek is the type locality, and "ensis" (Latin) means "belonging to".

Diagnosis. The Bullock Creek humerus is distinguished from *Aquila audax, A. chrysaetos* and *A. fasciata* by the following features:

The tuberculum supracondylare ventrale is flat in the fossil, but sits along the side of a raised shelf in *A. audax, A. chrysaetos* and *A. fasciata*, making the latter taxa relatively craniocaudally deeper compared to the length of the processus flexorius.

The two attachments of M. extensor metacarpi radialis proximal of the epicondylus dorsalis lie adjacent to each other in a dorsoventral line nearly perpendicular to the long axis of the shaft. In *A. audax* and *A. chrysaetos*, both pits are prominent and separate. In the fossil and *A. fasciata*, there is a single pit dorsally and a rugose scar ventrally.

The sulcus scapulotricipitalis is deeper than in *A. audax* and *A. chrysaetos* because the dorsal bordering ridge is more strongly developed. The condition in *A. fasciata* is similar to that of the fossil, although this may be size related.

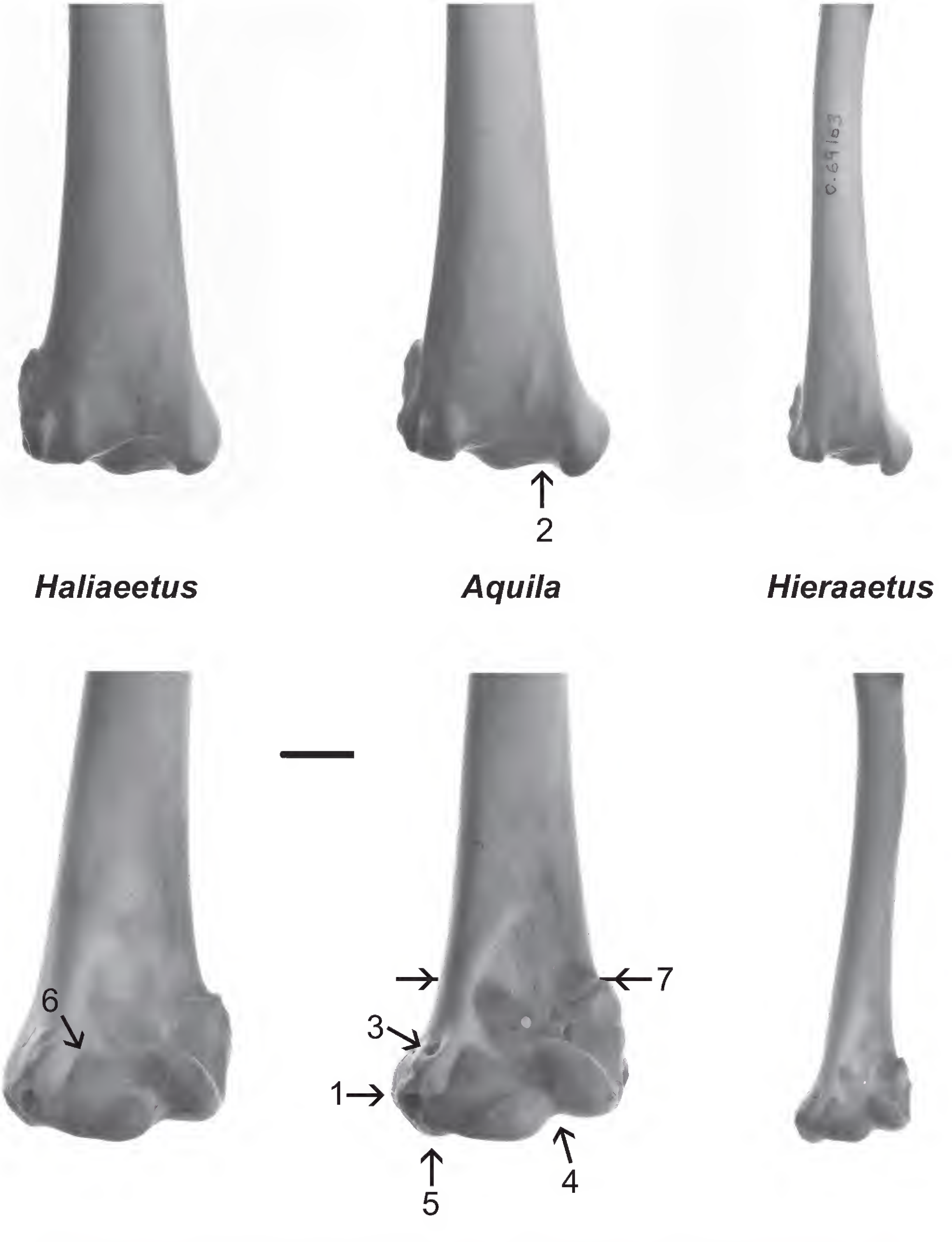

Figure 2. Distal humeri of extant Australian eagles; upper, caudal view; lower, cranial view. (*A*), *Haliaeetus leucogaster*. (*B*), *Aquila audax*. (*C*), *Hieraaetus morphnoides*. Bar equals 10 mm. Numbers refer to characters used to separate *Haliaeetus* from *Aquila-Hieraaetus* (see text). Character 7 show the points at which the shaft width measurement was taken proximal of the epicondylus dorsalis.

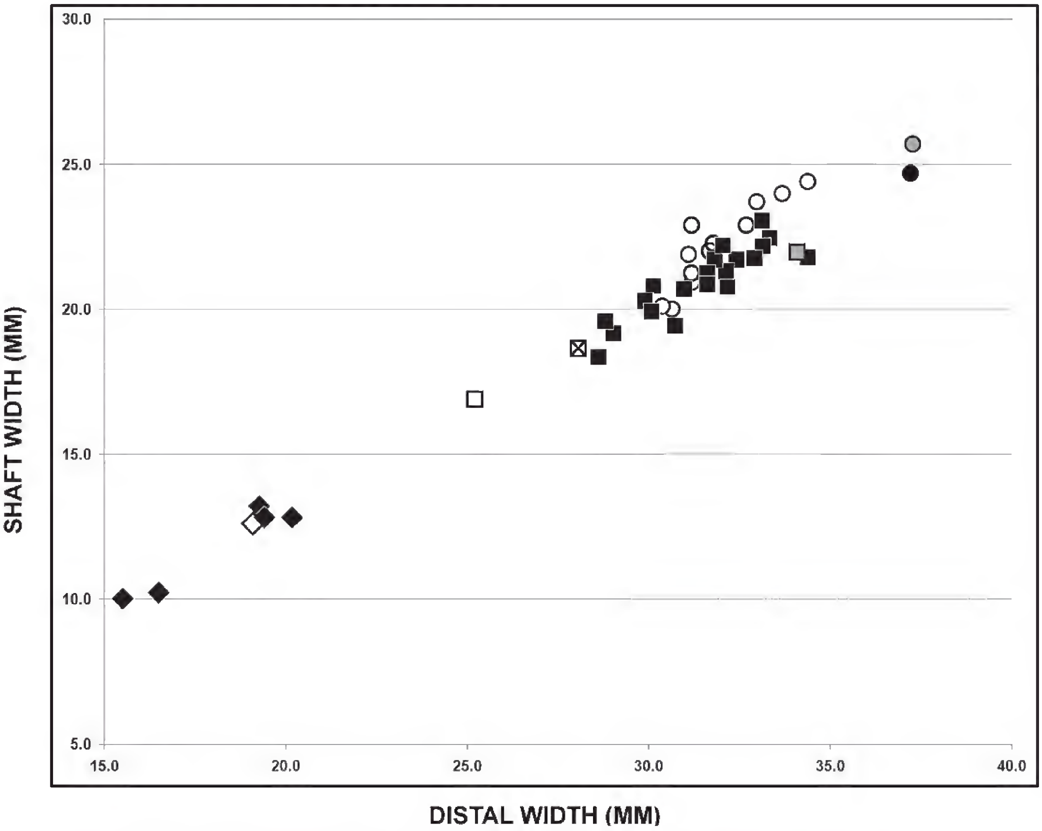

Figure 3. Shaft and distal widths (mm) of Bullock Creek humerus compared to those of extant eagles. Squares, *Aquila*: crossed, *A. bullockensis*; black, *A. audax*; grey, *A. chrysaetos*; open, *A. fasciata*. Diamonds, *Hieraaetus*: black, *H. morphnoides*; open, *H. pennatus*. Circles, *Haliaeetus*: black, *H. albicilla*; grey, *H. leucocephalus*; open, H. leucogaster.

The epicondylus dorsalis in the fossil does not project as far dorsally as in *A. audax, A. chrysaetos* and *A. fasciata*.

The fossil is smaller than specimens of *A. audax* and *A. chrysaetos*, but larger than that of *A. fasciata* examined here (Table 1; Fig. 3). Louchart *et al.* (2005) provided distal width measurements for several living species of *Aquila*. In this feature, *A. bullockensis* is larger than *A. fasciata* and *A. rapax* (Tawny Eagle) and smaller than *A. chrysaetos* and *A. heliaca*/*adelberti* (Spanish/European Imperial Eagles). It is in the range of *A. nipalensis* (Steppe Eagle). The distal depth of the humerus of *A. bullockensis* (14.1 mm) is well outside the range of *A. nipalensis*, as given by Louchart *et al.* (2005) (14.9–16.5 mm; n = 5). As many species of the Accipitridae in general, and *Aquila* in particular, display sexual dimorphism, however, size is not useful in distinguishing between taxa, and the fossil is only somewhat smaller than the smallest individuals of *A. audax*.

Description

Measurements: distal width 27.7 mm; width of shaft proximal to epicondylus dorsalis 18.5 mm; greatest width of brachial depression 9.4 mm; distal depth through condylis dorsalis 14.1 mm. The specimen preserves the distal end of the humerus, with the shaft broken above the fossa m. brachialis. In lateral view, the shaft is anteroposteriorly curved. In addition to those cited above, the fossil has the following features. The fossa m. brachialis is round and deep distally, and pointed proximally. The incisura intercondylaris is deep, narrow, and distally excavated in cranial view. The scars for M. pronator profundus and M. flexor carpi ulnaris on the epicondylus ventralis lie side by side; the former is noticeably deeper. In caudal view, the sulcus humerotricipitalis is shallow and wide. The sulcus scapulotricipitalis is narrow, with both sides of the groove at equal height in distal view. The fossa olecrani is shallow. In caudal view, the processus flexorius is bulbous, extending laterally from the shaft (Fig. 4).

Discussion

Milne-Edwards (1871, 1892) described several species that he placed in *Aquila*. These were subsequently moved by Lambrecht (1933) to a new genus, *Aquilavus*. Since then, a number of fossils have been initially described in *Aquila*, with many since transferred to other genera, some not even in the Accipitridae. Of those paleospecies that appear correctly assigned, the oldest are *A. delphinensis* and *A. pennatoides*, both described by Gaillard (1938) from Middle/Late Miocene deposits of Grive-Saint-Alban, France. *Eutolmaëtus edwardsi* Sharpe, 1899 (= the original name, *Aquila minuta* Milne-Edwards, 1871, is preoccupied), from Middle-?Late Miocene of SW Europe belongs to either *Aquila* or *Hieraaetus*. Younger species are *A. bivia* (Late Pliocene of southern United States; Emslie & Czaplewski, 1999) and ?*Aquila fossilis* (Middle/Late Pleistocene of Monte Reale, Sardinia, Italy; Giebel, 1847). There are also

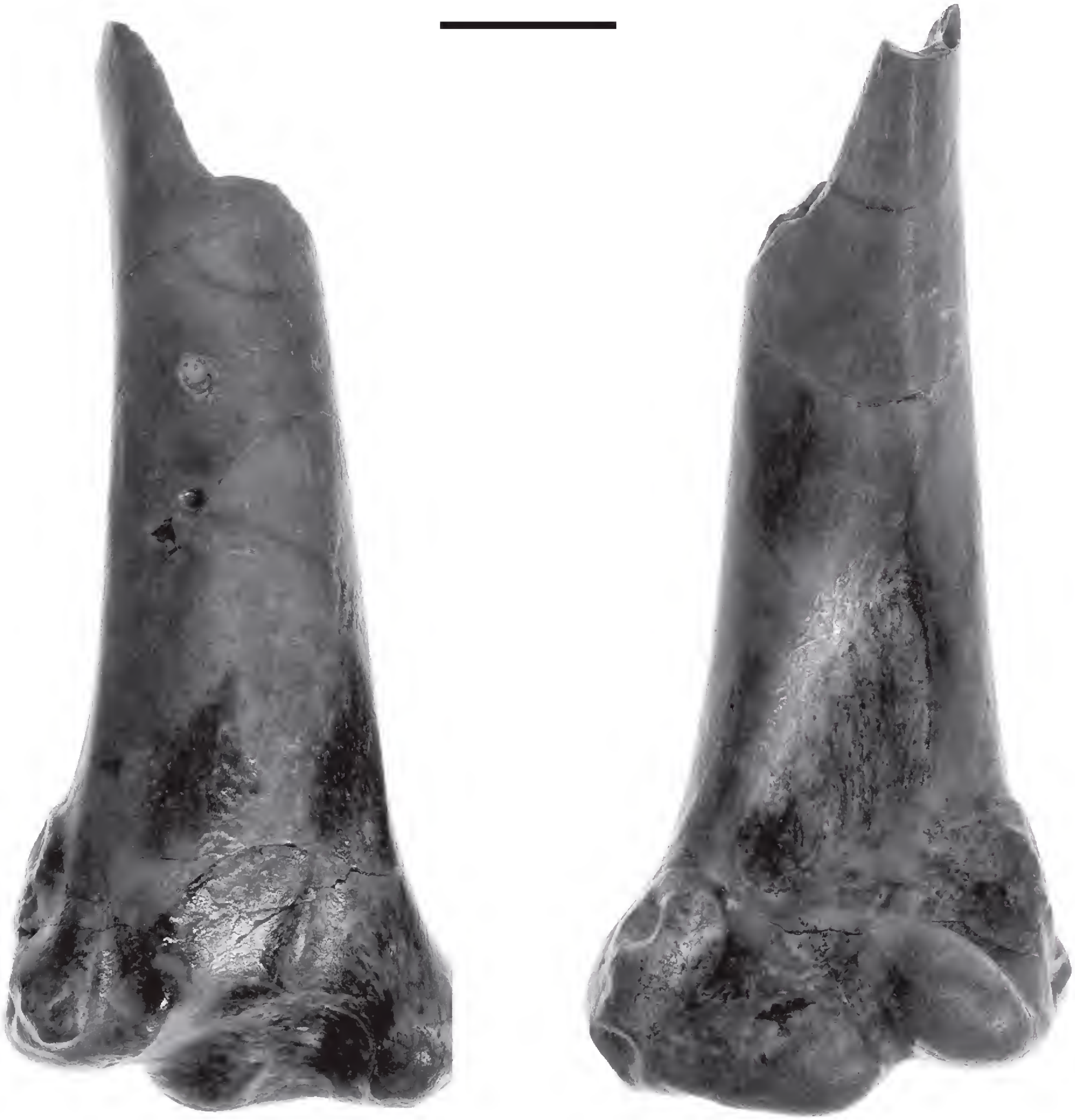

Figure 4. Distal right humerus of *Aquila bullockensis* (holotype QVM:2000:GFV:154). Left, caudal view; right, cranial view. Bar equals 10 mm.

Table 1. Distal width (DW) and shaft width (SW) measured just proximal of the processus epicondylus dorsalis (mm) and the ratio SW:DW for the fossil and extant species of *Aquila, Hieraaetus* and *Haliaeetus*.

	n	distal width		shaft width		ratio SW:DW	
		range	mean±sd	range	mean±sd	range	mean±sd
Aquila bullockensis	1	27.7		18.5		0.67	
Aquila fasciata	1	25.2		16.9		0.67	
Aquila chrysaetos	1	34.1		22.0		0.65	
Aquila audax	23	28.6–34.4	31.3±1.5	18.4–23.1	20.9±1.2	0.63–0.70	0.67±0.02
Hieraaetus morphnoides	5	15.5–20.4	18.2±2.1	10.0–13.2	11.8±1.6	0.62–0.68	0.65±0.03
Hieraaetus pennatus	1	19.1		12.6		0.66	
Haliaeetus leucogaster	12	30.4–33.7	31.9±1.3	20.0–24.4	22.2±1.5	0.66–0.73	0.69±0.02
Haliaeetus leucocephalus	1	37.2		24.7		0.66	
Haliaeetus albicilla	1	37.3		25.7		0.69	

identifications of pre-Quaternary fossils only to generic level (*Aquila* sp.) from the Miocene and Pliocene of several sites in Europe (Salotti *et al*., 2000; Mlíkovský, 2002). Fossil Pleistocene taxa of *Aquila* were discussed by Louchart *et al*. (2005). Unfortunately, none of the Tertiary paleospecies is represented by a humerus, and therefore it is not possible to compare the Bullock Creek fossil with any these.

Whether *A. bullockensis* represents an ancestor to *A. audax* is a matter for speculation with such limited fossil material. It comprises the oldest record of this genus in Australia, and possibly the oldest in the world. Other accipitrine material is known from the Camfield Beds deposits, but has not yet been studied. At least one specimen, an ulna, may represent this taxon.

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First Record of *Palaelodus* (Aves: Phoenicopteriformes) from New Zealand

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ABSTRACT. The first record of the flamingo-like Palaelodidae (Phoenicopteriformes) is reported from the Early Miocene, St Bathans Fauna of Central Otago, New Zealand. Two distal tibiotarsi are described as a new *Palaelodus* species and a cranial fragment of a sternum is tentatively assigned to the same taxon. The new species is slightly smaller than *P. wilsoni* from the Late Oligocene-Early Miocene of Australia, and is distinguished from all congeners by a more robust shaft with a gradual expansion of width to the distal condyles.

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> "*... it is the 'first' that fixes the peg upon which he can hang all the subsequent and, we hope, oft-repeated contacts that eventually grow into a real understanding. The "first" has to come first in avian paleontology likewise and, sad to relate, that first may be restricted to a single bone or a mere fragment thereof.*" (Loye Miller, 1950: 69).

Palaelodidae is an extinct family of long-legged aquatic birds presently considered to be the sister taxon of flamingos (Phoenicopteridae; Cheneval, 1983a; Heizmann & Hesse, 1995; Mlíkovský, 2002; Mayr, 2005). Known from Europe, Egypt, North and South America and Australia, they were first recognized when Milne-Edwards (1863) described *Palaelodus ambiguus, P. crassipes* and *P. gracilipes* from St Gérand-le-Puy, of Aquitanian, European Mammal Neogene Reference Level MN 2a, or Early Miocene, age (Cheneval, 1983a). Later, Milne-Edwards (1867–1871) described two further species, *P. minutus* and *P. goliath.* Lambrecht (1933) synonymized *P. minutus* with *P. gracilipes*, a move not followed by Brodkorb (1963) or Švec (1981). However, Cheneval (1983a) accepted this synonymy when he revised the palaelodids from St Gérand-le-Puy, listing three species of *Palaelodus* in the Aquitanian deposits (*Palaelodus ambiguus, P. crassipes, P. gracilipes*) and transferring *Palaelodus goliath* to *Megapaloelodus* A.H. Miller, 1944.

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All four species were recognized by Heizmann & Hesse (1995), in the mid-Miocene fauna from Nördlinger Ries (MN 6) and just *P. crassipes* and *M. goliath* in the fauna from the Steinheimer Basin (MN 7) in Germany. Recently, Mayr & Smith (2002) described the new genus and species *Adelalopus hoogbutseliensis* for the largest and oldest (earliest Oligocene, MP 21), European palaelodid.

In a recent treatment of the European palaelodid fauna, Mlíkovský (2002) synonymized *Megapaloelodus* A.H. Miller with *Palaelodus* Milne-Edwards and *P. gracilipes* (including *P. minutus*) and *P. crassipes* with *P. ambiguus*, stating that "…the alleged morphological differences between *Palaelodus gracilipes, P. ambiguus*, and *P. crassipes* pointed out by Cheneval (1983a) and Heizmann & Hesse (1995) are clearly size dependent, and can be interpreted as intra-specific variability" (Mlíkovský, 2002: 106). The systematic and taxonomic treatment of many species adopted by Mlíkovský (2002) often differs from others and has attracted much criticism (e.g., Mourer-Chauviré, 2004). However, the large dataset presented by Cheneval (1983: fig. 1), provides a size distribution consistent with only two species of palaelodid in St Gérand-le-Puy, where *P. gracilipes* and *P. crassipes* are just small and large examples of *P. ambiguus*, and published differences do appear to be potentially of an allometric nature. In the absence of a comprehensive examination of the variation represented by these European palaelodids Mlíkovský's (2002) synonymies are premature, so four species of *Palaelodus* existed contemporaneously in Europe, although this total may ultimately be reduced to two.

Palaelodids range in age in Europe from the early Oligocene of Belgium (Mayr & Smith 2002), through the Late Oligocene to the Middle Miocene of France, Germany and Bohemia in the Czech Republic (Milne-Edwards, 1863, 1867–1871; Lambrecht, 1933; Švec, 1981; Cheneval, 1987; Heizmann & Hesse, 1995; Mlíkovský, 2002). Outside Europe, two undetermined species are reported from the early Oligocene of Egypt (Rasmussen *et al.*, 1987). The family is represented in North America by *Megapaloelodus connectens* A.H. Miller, 1944 from the Early Miocene of South Dakota (A.H. Miller, 1944; L. Miller, 1950, 1952) and *M. opsigonus* Brodkorb, 1961, from the Pliocene of Oregon (Brodkorb, 1961). In South America, *Megapaloelodus* has been recorded from the Late Miocene of Argentina (Noriega, 1995) and *Palaelodus* cf. *P. ambiguus* from the late Oligocene—Early Miocene of Taubuté Basin in Brazil (Alvarenga 1990, *fide* Mayr, 2009).

Phoenicopteriforms are significant components of the Australian Oligo-Miocene to Pleistocene lacustrine faunas. Several taxa of true flamingos (A.H. Miller, 1963; Rich *et al.*, 1987, 1991; Vickers-Rich, 1991) and two species of palaelodids, a smaller *Palaelodus pledgei* Baird & Vickers-Rich, 1998 and a larger *P. wilsoni* Baird & Vickers-Rich, 1998, are relatively abundant (Baird & Vickers-Rich, 1998; Boles, 2006). Both palaelodids are found in the Oligo-Miocene Etadunna and Namba Formations of South Australia. A single specimen from Pleistocene deposits in Cooper Creek, South Australia, was attributed to *P. wilsoni*, making it the youngest record for the family (Baird & Vickers-Rich, 1998). This specimen was recently re-evaluated, and while confirmed as a palaelodid, it is doubtful whether it is conspecific with *P. wilsoni* (Worthy, 2008).

In both Northern and Southern Hemispheres, palaelodids usually derive from lacustrine deposits and are known from abundant material in some localities (Cheneval, 1983a; Heizmann & Hesse, 1995; Mlíkovský, 2002; Mayr, 2005). Nevertheless, their biology and ecology are poorly known. They have long tarsometatarsi (though not so long as in flamingos), which are laterally compressed and associated with other modifications of the leg that Cheneval (1983a) and Cheneval & Escuillié (1992) interpreted as adaptations for diving. However, no diving birds have elongate legs, and the stated modifications of the leg, laterally compressed shaft of the tarsometatarsus and enlarged cnemial crest of the tibiotarsus, would equally facilitate pushing a leg through deep water while wading. A laterally compressed tarsometatarsus would be unique in waders and alternatively could be explained by a shared ancestry with grebes (Podicipedidae), because these birds also have compressed tarsometatarsi (e.g., Mayr, 2004). Flamingos, to which palaelodids are most closely related, are now known to be the sister taxon to grebes based on robust genetic data and morphological traits (van Tuinen *et al.*, 2001; Mayr, 2004; Hackett *et al.*, 2008). The cranium of *Palaelodus* has been described by Cheneval & Escuillié (1992). It confirms the phylogenetic affinity of *Palaelodus* and flamingos, but shows palaelodids had a superficially crane-like premaxilla markedly different from flamingos. But unlike cranes, *Palaelodus ambiguus* had a deep mandible, interpreted by Cheneval & Escuillié (1992) to mean it had a filter-feeding apparatus as is well known in flamingos. Also, *Palaelodus* had well-developed salt glands indicating an ability, shared with flamingos, to feed in saline waters. These observations suggest that *Palaelodus* was a wading bird capable of obtaining food from saline waters. The coexistence of a diversity of flamingos and palaelodids in Australia for most of the Neogene is doubtless related to the widespread availability of extensive shallow saline lakes throughout this period (Pledge & Tedford, 1990; Woodburne *et al.*, 1994; Alley, 1998).

The St Bathans Fauna was recently named and described from the upper Early Miocene (19–16 Ma) Bannockburn Formation, Manuherikia Group in Central Otago, New Zealand (Worthy *et al.*, 2007). The source beds are lacustrine in nature and their extent and nature indicates a paleolake some 5600 km^2 in area with deltaic river facies entering it (Douglas, 1986; Pole *et al.*, 2003). The avifauna of the St Bathans Fauna is dominated by anseriforms, with a minimum of eight taxa in five genera (Worthy *et al.*, 2007, 2008). The avifauna also comprises such diverse taxa as tubenoses (Procellariiformes), birds of prey (Accipitriformes), rails (Rallidae) and another as yet unidentified representative of Gruiformes, gulls (Laridae) and Charadriiformes with features of typical waders, a heron (Ardeidae), pigeons (Columbidae), parrots (Psittaciformes), swiftlets (Apodidae), owlet-nightjars (Aegothelidae) and passerine birds (Passeriformes). Fish, frogs, reptiles and mammals are also represented. This lake provided suitable habitat for wading birds, so given the temporal relativity and geographic proximity with Australian Oligo-Miocene faunas, phoenicopteriforms might also be expected. The purpose of this contribution is to describe such a discovery, the first record of a palaelodid from New Zealand, which is significant for the ecological reconstruction of paleo-Lake Manuherikia and the New Zealand avifauna in general.

The St Bathans Fauna provides the first insight into the terrestrial fauna resident on that part of Zealandia that is now New Zealand for the entire Tertiary. Zealandia is the India-sized area of continental crust that encompasses New

Caledonia, Chatham Islands, New Zealand and Macquarie Island (Campbell & Hutching, 2007; Goldberg *et al.*, 2008). New Zealand has long been thought to have a vicariant component to its fauna (Fleming, 1979; Stevens, 1980; Gibbs, 2006), but recently the controversial suggestion that Zealandia was entirely submerged during the Late Oligocene 25–22 Ma, requiring the entire terrestrial biota to have been derived by colonization following long-distance over-water dispersal, has been vigorously debated (Pole, 1994; Gibbs, 2006; Heads, 2006; Waters & Craw, 2006; Campbell & Hutching, 2007; Knapp *et al.*, 2007; Ladiges & Cantrill, 2007; Trewick *et al.*, 2007; Goldberg *et al.*, 2008; Landis *et al.*, 2008; McDowall, 2008). The St Bathans Fauna provides direct evidence of the composition of the terrestrial biota just 3–4 million years after the maximal submergence of Zealandia, so the endemicity and relatedness of that biota to those of Australia, the presumed major source of dispersed taxa, is crucial to understanding the history of Zealandia's biota.

Methods

Abbreviations: *LF*, Local Fauna; *L*, left; *Ma*, million years ago; *R*, right. Institutions: *CM*, Canterbury Museum, Christchurch, New Zealand; *MV*, Museum Victoria, Melbourne, Victoria, Australia; *NMNZ*, Museum of New Zealand Te Papa Tongarewa, Wellington (formerly National Museum of New Zealand, Dominion Museum, and Colonial Museum), New Zealand; *SAM*, South Australian Museum, Adelaide, South Australia, Australia; *UCMP*, University of California, Museum of Paleontology, Berkeley, California, USA.

Names for specific bone landmarks follow the anatomical nomenclature of Baumel & Witmer (1993) with English translations thereafter, or Howard (1929).

Comparative material

Below we specify only the phoenicopteriform material of immediate relevance to our comparisons. For the Australian fossils, we give age, local fauna and locality details to allow interpretation of their temporal range.

Palaelodidae

Palaelodus wilsoni Baird & Vickers-Rich, 1998, Oligo-Miocene: SAM P.22706, distal R tibiotarsus (+imperfect L tarsometatarsus), Croc Pot Point (Minkina LF), Lake Palankarinna (Baird & Vickers-Rich, 1998) (informally also known as Tortoise Hole Locality, pers. comm. Neville Pledge 11 July 2008); SAM P.27973, distal L tibiotarsus, Mammalon Hill (Ngama LF), Lake Palankarinna; SAM P.41250, distal R tibiotarsus, SAM North (Ditjimanka LF), Lake Palankarinna. MV P. 187012, distal R tibiotarsus, Lake Palankarinna; MV P. 187018, distal L tibiotarsus, Neville's Nirvana, Lake Palankarinna.

Palaelodus ?wilsoni, Pleistocene: SAM P.25151, distal R tibiotarsus, Cooper Creek, South Australia (Worthy, 2008).

Palaelodus pledgei Baird & Vickers-Rich, 1998, Oligo-Miocene: SAM P.27997, proximal R tarsometatarsus, paratype, Croc Pot Point, UCMP Site 3 (V5762) (Minkina LF), Lake Palankarinna (Baird & Vickers-Rich, 1998); SAM P.42002, distal R tibiotarsus, SAM North Quarry, Lake Palankarinna, Lake Eyre Subbasin, South Australia.

Palaelodus ambiguus Milne-Edwards, 1863, Oligo-Miocene: CM Av11394, L tibiotarsus; CM Av11396, R tibiotarsus, St Gérand-le-Puy, France.

Phoenicopteridae

Phoenicopterus chilensis Molina, 1782, modern: SAM B.25448, South America.

Phoenicopterus ruber Linnaeus, 1758, modern in Africa, Europe, Asia, Caribbean, South America; extinct Australia, Pliocene (A.H. Miller, 1963): SAM B.11552.

The following Australian fossil flamingos (A.H. Miller, 1963; Rich *et al.*, 1987) were examined to more completely assess distribution of characters diagnostic of palaelodids.

Phoenicopterus novaehollandiae A.H. Miller, 1963, Oligo-Miocene: SAM P.39231, R tibiotarsus, Mammalon Hill, Lake Palankarinna, Etadunna Formation, South Australia.

Ocyplanus proeses de Vis, 1905, Pliocene: SAM P.35225, cast of referred distal R tibiotarsus, originally described as *Phoeniconaias gracilis* A.H. Miller, 1963, collected Stirton Quarry, = Site 1, UCMP V-5772, Lake Kanunka, Lake Eyre Subbasin, South Australia.

Xenorhynchopsis tibialis de Vis, 1905, Pleistocene: SAM P.35226, cast of lectotype distal R tibiotarsus, Cooper Creek.

Xenorhynchopsis minor de Vis, 1905, Pleistocene: SAM P.35227, cast of holotype, distal R tibiotarsus, collected at Unduwumpa (a Gregory Site), Cooper Creek.

Results

Systematic Paleontology

Order Phoenicopteriformes Sharpe, 1891

Family Palaelodidae (Stejneger, 1885)

Genus *Palaelodus* Milne-Edwards, 1863

The new species described here for NMNZ S.51258 is referred to Palaelodidae because of the following unique combination of characters derived from Lydekker (1891), L. Miller (1950), Švec (1981), and Baird & Vickers-Rich (1998) (Figs 1, 2): (1) the lateral tuberosity for the attachment of the *retinaculum extensorium tibiotarsi* is approximately circular and prominent, located laterally to the *pons supratendineus* (supratendinal bridge) and separated from the lateral margin of the bone and from the proximal margin of the *incisura intercondylaris*; (2) the intercondylar incision is deep, broadens proximally and extends into proximo-medial face of medial condyle; (3) the *sulcus extensorius* is located centrally on the shaft, is narrow (a third of shaft width) and deep; (4) the proximal end of the supratendinal bridge is widely separated from the medial margin of the shaft by a robust rounded ridge; (5) the supratendinal bridge is not elongate; (6) the *condyli lateralis et medialis* have deep tendinal pits just caudad of their cranial projections; (7) the distal margins of the lateral and medial condyles are distinctly notched; (8) the distal cranial part of the medial condyle is markedly inflated medially; (9) the *trochlea cartilaginis tibialis* has a prominent medial ridge; (10) the medial edge of the supratendinal bridge is excavated in a furrow separating it from the medial margin; (11) the intercondylar incision lacks a prominent distally directed articular facet for the *eminentia intercotylaris* of the tarsometatarsus, i.e. the "anterior intercotylar tubercle" of Švec (1981).

We note the following additional tibiotarsal characters that further define this family: (12) the medial attachment for the *retinaculum extensorium tibiotarsi* forms a low rounded zone on the medial side of the *sulcus extensorius* just proximal to the tendinal bridge; (13) the lateral and medial condyles lack significant projection caudad of the shaft; (14) in cranial view, the cranial part of the medial condyle is displaced medially such that it is entirely mesad of the supratendinal bridge resulting in a relatively wide notch between the condyles.

Of these characters, we consider character 1 an autapomorphy of the Palaelodidae: in no other birds is the lateral attachment of the *retinaculum extensorium tibiotarsi* a prominent, near circular, tuberosity: it is usually elongate and located near the margin of the extensor sulcus. Baird & Vickers-Rich (1998) used three of these characters to distinguish flamingos from palaelodids as follows (character number above to which these relate): intercondylar incision, shallower, not so deeply extending into proximo-medial face of medial condyle (2); distal tendinal pits shallower (6); notches in distal margins of lateral and medial condyles shallower (7). However, we found the expression of these characters variable intra- and/or interspecifically, and so treat them as synapomorphies of Phoenicopteridae and Palaelodidae, rather than as autapomorphies of Palaelodidae. Further, while Baird & Vickers-Rich (1998) stated that the distal opening of the extensor canal is rounded and narrow in *Palaelodus* but rounded and broad in flamingos, we find this difference to be inconsistent. While the combination of characters 1–14 is unique to palaelodids, apart from character 1, individually, all the other characters are either present convergently in some other families or are plesiomorphic in palaelodids.

Flamingos differ from palaelodids including the new species described below as follows: the lateral attachment of the *retinaculum extensorium tibiotarsi* is an elongate crest, linked to, or closely approaching, an elevated, distally directed articular facet for the intercotylar eminence of the tarsometatarsus; the medial attachment for the extensor retinaculum is a prominent crest on the ridge medially of the extensor sulcus; the extensor sulcus is wider and more laterally located; the medial bounding ridge is narrower; the supratendinal bridge is more elongate; the lateral and medial condyles project significantly caudad of the shaft; the distal anterior part of the medial condyle is not inflated medially; the medial condyle is not so far offset medially, so it lies distad and in line with the tendinal bridge, resulting in a narrower anterior notch between the condyles; the *trochlea cartilaginis tibialis* lacks a prominent medial ridge.

In other large birds with some similarity to palaelodids, the lateral attachment for the extensor retinaculum, if present, is not circular (e.g., ardeids, pelecanids, threskiornithids, and ciconiids), but more elongate, and in those birds with elongate tibiotarsi (e.g., species of *Grus, Ciconia, Ardeotis*), the lateral attachment for the extensor retinaculum is always associated with an intercondylar tubercle, an elevated distally directed prominent facet for articulation with the intercotylar eminence of the tarsometatarsus, see character 101 of Mayr & Clarke (2003), which is presumed to act as a locking mechanism in the tibial-tarsal joint.

The fossil is referred to *Palaelodus* as it does not differ from members of this genus to any significant degree (Cheneval, 1983a; L. Miller, 1950; Baird & Vickers-Rich, 1998). *Megapaloelodus connectens* A.H. Miller, 1944 is a much larger species and was distinguished by deeper distal notches in the medial condyle (L. Miller 1950). The European species *P. goliath* was referred to *Megapaloelodus* solely on size, and if Mlíkovský's (2002) synonymy of *Megapaloelodus* with *Palaelodus* is accepted, then the family had only one globally-distributed genus during the Miocene.

Palaelodus aotearoa n.sp.

Figs 1–3

Holotype. NMNZ S.51799, a distal right tibiotarsus, collected 10 February 2009 by the University of New South Wales, NSW, Australia/Canterbury Museum, Christchurch, NZ/ Museum of New Zealand Te Papa Tongarewa, Wellington, NZ expedition.

Diagnosis. A *Palaelodus* species within the size range of *P. wilsoni* and *P. ambiguus* (Tables 1, 2) but tibiotarsus with a relatively broader shaft for its distal width, a less concave medial margin above the medial condyle, and a broader extensor sulcus that is more widely separated from the medial margin.

Etymology. For Aotearoa, a Maori name for New Zealand.

Measurements of holotype. Distal width 13.9 mm, craniocaudal depth of lateral condyle 13.7 mm, craniocaudal depth of medial condyle 14.8 mm, shaft width proximal side tendinal bridge 10.2 mm, minimum shaft width 7.5 mm, preserved length 81.6 mm.

Paratype (Figs 2, 3). NMNZ S.51258, a distal right tibiotarsus, collected 12 January 2008 by the University of New South Wales, NSW, Australia/University of Adelaide, South Australia/Canterbury Museum, Christchurch, NZ/ Museum of New Zealand Te Papa Tongarewa, Wellington, NZ expedition.

Measurements of paratype. Distal width 13.7 mm, craniocaudal depth of lateral condyle 13.9 mm, craniocaudal depth of medial condyle 15.0 mm, shaft width proximal side tendinal bridge 9.7 mm, minimum shaft width preserved 9.1 mm, preserved length 25.0 mm.

Holotype locality. Bed HH1b, 9.5–9.58 m above base of the Bannockburn Formation, Trench Excavation, foot of hill 50 m across terrace from river bank at 44.90780° S; 169.85844° E, Manuherikia River, Home Hills Station, Otago, New Zealand; ca. 10–15 cm thick sand & cobble layer; Fossil Record Number in the archival Fossil Record File of the Geological Society of New Zealand H41/f0103.

Table 1. Distal and shaft widths (mm) of tibiotarsi for *Palaelodus* species, European taxa after Cheneval (1983a).

species	distal width mean (range) s.d., n	shaft width mean (range) s.d., n	SW/DW
Palaelodus gracilipes	11.1 (9.7–12.2) 0.19, 77	5.8 (5.0–6.7) 0.17, 41	52.2%
Palaelodus ambiguus	12.5 (10.6–20.0) 0.68, 316	6.6 (4.8–9.1) 0.27, 200	52.8%
Palaelodus crassipes	14.9 (14.0–16.2) 0.49, 8	7.9 (7.3–8.3) 0.13, 5	53.0%
Megapaloelodus goliath	18.1 (16.7–20.4) 1.06, 17	8.2 (7.6–9.0) 0.24, 6	45.3%
Palaelodus aotearoa S.51799	13.9	7.5	53.9%

Table 2. Measurements (mm) of tibiotarsi of *Palaelodus aotearoa* compared to selected *Palaelodus* species. Depth of the lateral and medial condyles is in craniocaudal plane. SW1 and SD1 were measured at a point twice the distance the proximal side of the supratendinal bridge was from the distal end. SW2 is taken level with the proximal margin of the supratendinal bridge. Abbreviations: DW is distal width, MC is medial condyle, LC is lateral condyle, SW is shaft width.

specimens	DW	LC depth	MC depth	SW min	SW1	SD1	SW2	MC/DW depth	SW1/DW	SW2/DW
Palaelodus wilsoni										
SAM P.22706	16.5	15.9	17.7	7.4	7.6	6.1	—	107.3	46.1	—
SAM P.27973	14.6	13.3	15.4	—	—	—	8.4	105.5	—	57.5
SAM P.41250	—	—	—	7.3	7.6	6.0	10.0	—	—	—
MV P.187018	ca. 17.2	—	18.7	7.7	7.7	6.3	11.2	108.7	44.8	65.1
MV P.187012	—	—	—	—	7.1	6.1	10.6	—	—	—
?*Palaelodus wilsoni*										
SAM P.25151	16.4	16.8	18.8	—	9.5	7.1	10.2	114.6	56.7	62.2
Palaelodus ambiguus										
CM Av11396	12.9	12.0	13.2	6.6	6.9	4.9	8.1	102.3	53.5	62.8
CM Av11394	14.0	13.5	14.8	6.8	7.0	4.7	8.1	105.7	50.0	57.7
Palaelodus aotearoa										
NMNZ S.51799	13.9	13.7	14.8	7.5	7.9	5.6	10.2	106.5	56.8	73.4
NMNZ S.51258	13.7	13.9	15.0	—	—	—	9.7	109.3	—	70.7

Paratype locality. Bed HH1a, 6.88–7.0 m above base of Bannockburn Formation, main quarry at 44.907944° S, 169.858222°E, Manuherikia River, Otago, New Zealand; Fossil Record Number in the archival Fossil Record File of the Geological Society of New Zealand H41/f88.

Stratigraphy/Age/Fauna. Bannockburn Formation, Manuherikia Group, Early Miocene (Altonian); 19–16 Ma; St Bathans Fauna.

Description and comparisons. Both NMNZ S.51799 and NMNZ S.51258 are stained black and have slightly worn edges to the condyles (Figs 1, 2), consistent with the transported and disarticulated nature of specimens in both deposits and are inferred to have been accumulated in the sublittoral zone. Their distal widths are within the size range for the Australian *P. wilsoni* and the European *P. ambiguus*, indicating a medium-sized palaelodid (Table 1). To capture the observation that in *P. aotearoa* the shaft expands in width more gradually towards the condyles and is relatively wider than in other taxa, three different width measurements were taken (Table 2). A standard least shaft width measurement, only ascertainable for NMNZ S.51799, was 53.9% of distal width in *P. aotearoa*, a ratio higher than the ratio of the means for the European palaelodid species, and higher than values for *P. ambiguus* (CM specimens), or for *P. wilsoni* individuals. Secondly, we measured width and depth values (SW1 and SD1) of the shaft where the distance to the proximal side of the supratendinal bridge was half that to the distal end (Table 2). Thirdly, we measured shaft width at the proximal end of the supratendinal bridge (SW2; Table 2). Values for SW2 relative to distal width (SW2/DW) of 57.7 and 62.8% in specimens of *P. ambiguus* (Table 2) are about 7–9% greater than SW1/DW. Equivalent ratios for *P. wilsoni* (57–65%) are similar to those for *P. ambiguus* but less than the values of 70.7 and 73.4% for *P. aotearoa*. In summary, the tibiotarsal shaft of *P. aotearoa* is both relatively stouter than that of the European and Australian *Palaelodus* species and widens much more gradually towards the distal end, rather than abruptly to create a step in anterior view. *Palaelodus aotearoa* is substantially larger than *P. pledgei*, as revealed by the condylar width of the paratype tarsometatarsus SAM P. 27997 and a here referred distal tibiotarsus SAM P.42002.

Tentatively referred specimen. An additional probable phoenicopteriform specimen was found in 2008 in bed HH1a. NMNZ S.51257 is a fragment of the cranial part of a sternum (Fig. 4), 23.2 mm wide and preserving the base of the carina, about 14 mm of the left and 11 mm of the right *sulcus articularis coracoidei*, and dorsally the medial part of the *pila coracoidea*. On this fragment the left coracoidal sulcus overlaps above the right sulcus medially, the coracoidal sulci are roughly in the same plane as the adjacent *labrum internum*, a *spina externa* is inferred by the presence of a preserved base, the ventral margin of the coracoidal sulci slope caudally rather than being near right angles to mid-line, the anterior margin of the *pila coracoidea* lacks a *spina interna* and has a broad central notch, and the carina has a broad base. The caudal margin of the *pila coracoidea* drops abruptly down onto the *pars cardiaca*, but little of this facies is preserved. Compared with other large carinate birds found to-date in the St Bathans Fauna, accipitrid sterna have a similar general form to the preserved fragment but differ with the anterior margin of the *labrum internum* forming a face at an abrupt angle to the adjacent coracoidal articular facet. Anseriforms and gruiforms, with the exception of *Balearica* (Mayr & Clarke, 2003), which differs markedly in shape from the fossil, differ markedly in having non-overlapping coracoidal sulci. Other large birds that might be expected in the New Zealand faunas all differ markedly. Some phalacrocoracids are similar with overlapping coracoidal sulci, but differ trenchantly by much thinner dorsoventral depth and that the labrum internum is developed as a prominent cranially directed facet to receive an opposing facet on the coracoid. In pelecanids, large procellariiforms, such as *Macronectes, Thalassarche*, and *Diomedia*, and in most ciconiids, the coracoidal sulci do not overlap and, in all these taxa, the labrum internum forms a large facet as seen in phalacrocoracids. The fragment is very similar in shape to the only published image of a palaelodid sternum that we are aware of, a cranial sternal fragment attributed to *Palaelodus* [=*Megapaloelodus*] *goliath* by Milne-Edwards (1867–1871: plate 87). It appears to be of appropriate size for *Palaelodus aotearoa*, based on relative sizes of *Phoenicopterus* distal tibia and sterna, so we tentatively refer it to the new taxon.

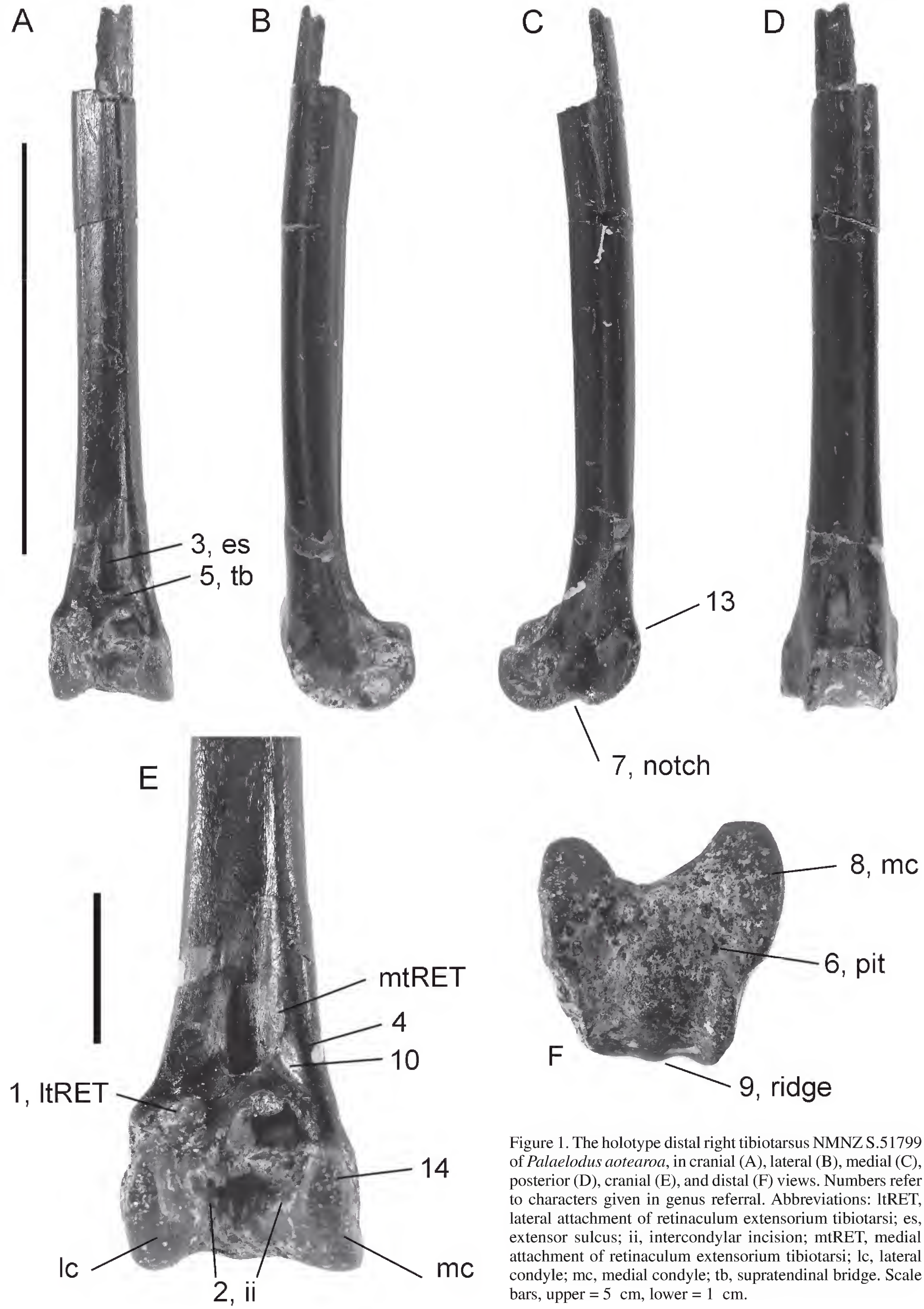

Figure 1. The holotype distal right tibiotarsus NMNZ S.51799 of *Palaelodus aotearoa*, in cranial (A), lateral (B), medial (C), posterior (D), cranial (E), and distal (F) views. Numbers refer to characters given in genus referral. Abbreviations: ltRET, lateral attachment of retinaculum extensorium tibiotarsi; es, extensor sulcus; ii, intercondylar incision; mtRET, medial attachment of retinaculum extensorium tibiotarsi; lc, lateral condyle; mc, medial condyle; tb, supratendinal bridge. Scale bars, upper = 5 cm, lower = 1 cm.

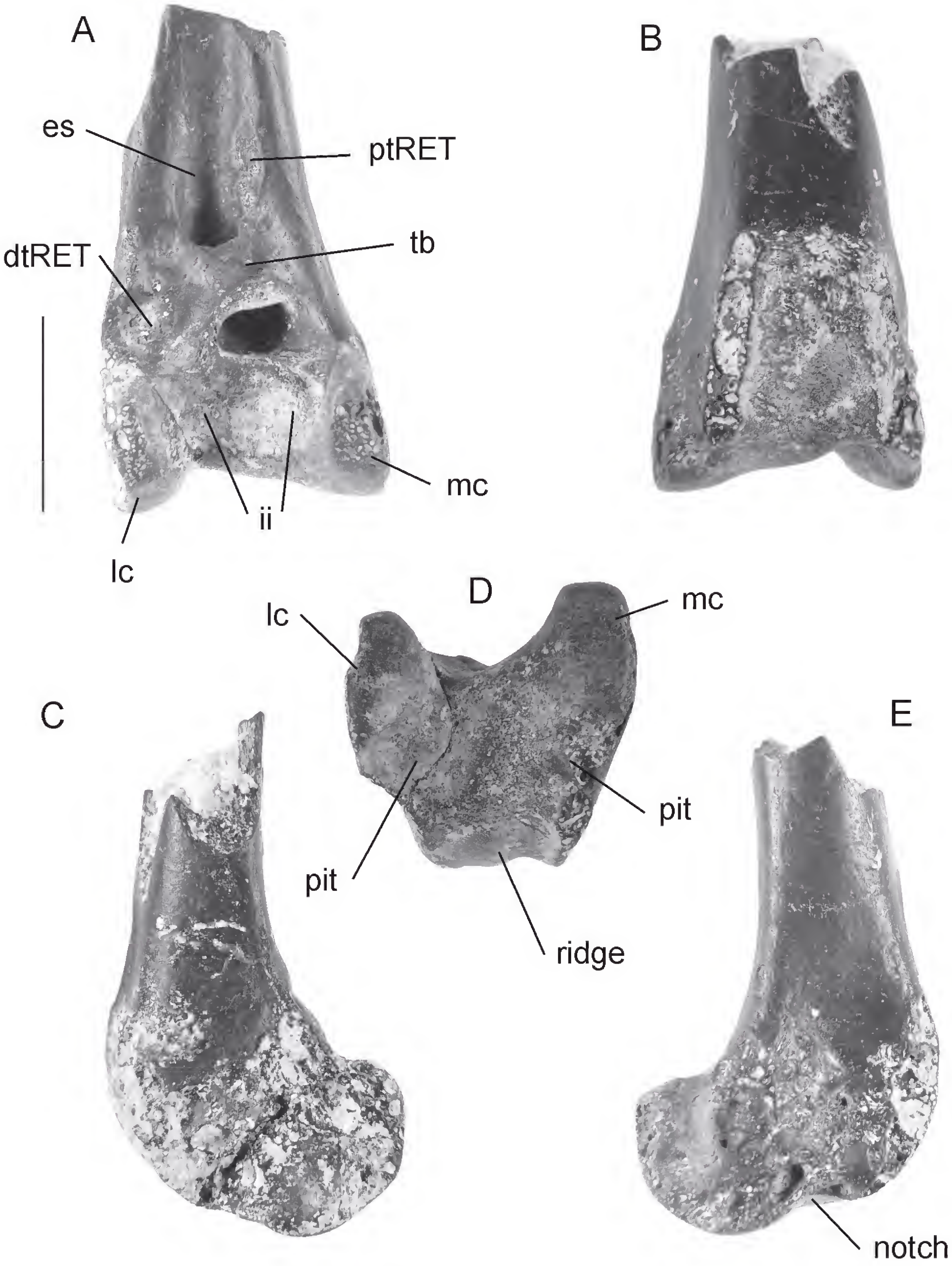

Figure 2. The paratype distal right tibiotarsus NMNZ S.51258 of *Palaelodus aotearoa*, in anterior (A), posterior (B), distal (C), lateral (D), and medial (E) views. Abbreviations as in Fig. 1. Scale bar = 1 cm.

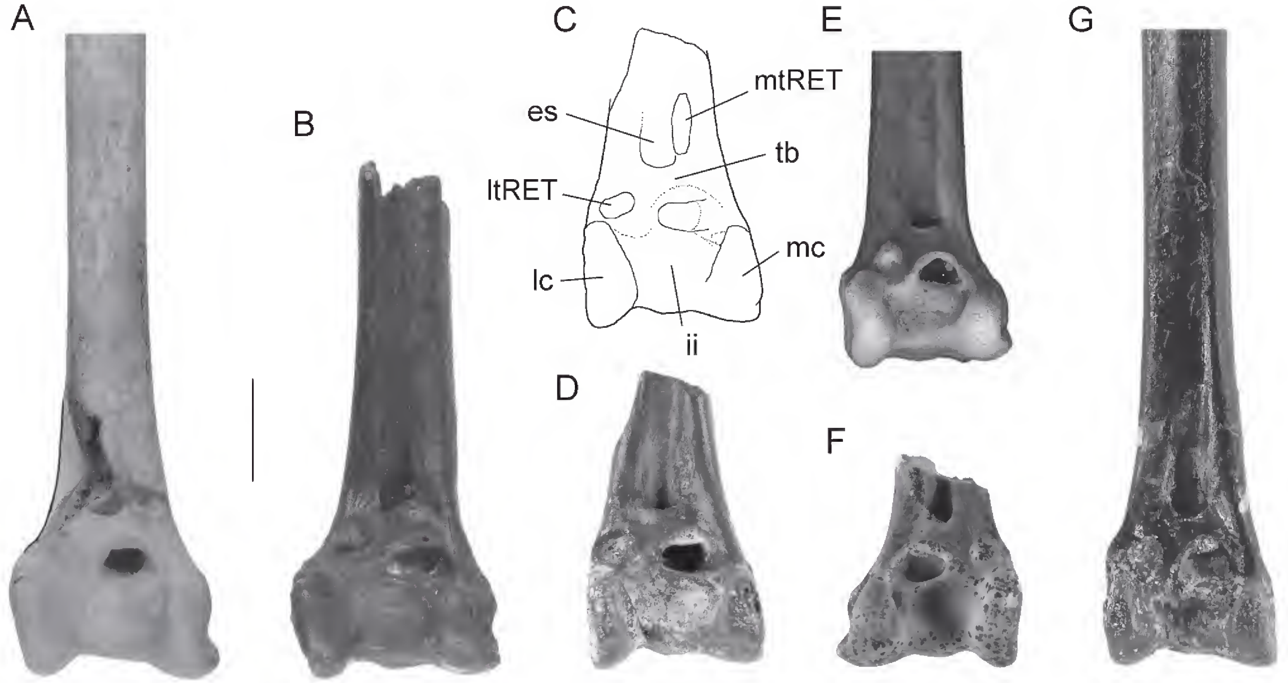

Figure 3. Distal tibiotarsi of *Palaelodus* species compared in cranial views: A, *P. wilsoni* SAM P.22706; B, *Palaelodus* sp. indet. SAM P.25151; C, D, *P. aotearoa* NMNZ S.51258; E, *P. ambiguus*, CM Av11396; F, *P. wilsoni*, SAM P.27973; and G, *P. aotearoa* NMNZ S.51799. A and F illustrate size range in *P. wilsoni*. Scale bar = 1 cm. Abbreviations as in Fig. 1.

Discussion

We report here the first fossil phoenicopteriform from New Zealand, based on two, or possibly three, fossil bones. The tibiotarsi fragments represent a species that can unambiguously be referred to the family Palaelodidae. They are described here as a new species *Palaelodus aotearoa*. Palaelodids had a global distribution in the Oligo-Miocene, with species in Australia (Baird & Vickers-Rich, 1998), Europe (Milne-Edwards, 1863, 1867–1871; Lambrecht, 1933; Švec, 1981; Cheneval, 1987; Heizmann & Hesse, 1995; Mayr & Smith, 2002; Mlíkovský, 2002), Egypt (Rasmussen *et al.*, 1987), North America (A.H. Miller, 1944; L. Miller, 1950, 1952; Brodkorb, 1961), and South America (Noriega, 1995). In Australia, *Palaelodus* is known from inland Oligo-Miocene (26–24 Ma) lacustrine deposits in the Etadunna and Namba Formations of South Australia by the two species *P. wilsoni* and *P. pledgei* (Baird & Vickers-Rich, 1998; Boles, 2006). The first of these is also recorded from Pleistocene deposits in Cooper Creek, South Australia (Baird & Vickers-Rich, 1998), and while the specific identity is questioned (Worthy, 2008), the generic referral is not doubted, making it the youngest record for the family. The New Zealand *Palaelodus aotearoa*, at 19–16 Ma in age, thus bridges this temporal gap for palaelodids in Australasia and provides evidence of a distinct lineage of palaelodids in New Zealand in the Early Miocene. The available material does not warrant a phylogenetic assessment of its relationships, but with its stouter shaft, it differs more from the Australian taxa than they do from the European ones. It is hoped that future discoveries will make such an assessment possible.

There is uncertainty about how many species of *Palaelodus* should be recognized in Europe. Apart from *Palaelodus goliath*, three species (*Palaelodus ambiguus, P. crassipes*, and *P. gracilipes*) are recognized (e.g., Cheneval, 1987; Heizmann & Hesse, 1995), although these were reduced to just one (*P. ambiguus*) by Mlíkovský (2002). Research to address the specific diversity of European palaelodids appears warranted, as acknowledged by Mayr (2009), as the data presented by Cheneval (1983a, fig. 1) shows variation across these three taxa that could be consistent with a single species. Moreover, for these three essentially identical "taxa" to have existed sympatrically and contemporaneously for about 12 million years from the Late Oligocene to the Middle Miocene (Heizmann & Hesse, 1995; Mlíkovský, 2002; Mayr, 2005) without divergence is less parsimonious than that they be considered a single taxon. Modern examples where congeneric taxa are nearly identical in skeletal morphology and differ by size are probably the result of very recent speciation events, for example the Australasian teal (Joseph *et al.*, 2009). If Mlíkovský's (2002) synonymy is supported by further research, only two palaelodids, *P. ambiguus* and *P. goliath* lived in sympatry in Europe, having been found together in many sites. In Australia, the two *Palaelodus* species had a similar size disparity, with *P. pledgei* smaller than European *P. gracilipes*, and *P. wilsoni* in the size range of European *P. ambiguus-P. crassipes. Palaelodus aotearoa* is much smaller than *P. goliath* or the *Megapaloelodus* spp., in the size range for *P. ambiguus* and at the small end of the range for *P. wilsoni*, indicating it is a medium-sized palaelodid.

The addition of *Palaelodus aotearoa* to the St Bathans Fauna significantly affects perception of the avian diversity (particularly of waterbirds) in Miocene New Zealand. Paleo-Lake Manuherikia (ca. 5600 km^2) supported a diverse community of waterbirds with waterfowl, wading charadriiforms, a heron (Ardeidae) and a palaelodid now known.

More than 3000 avian fossils have been prepared from the St Bathans Fauna and, as yet, true flamingos (Phoenicopteridae), cormorants (Phalacrocoracidae), darters

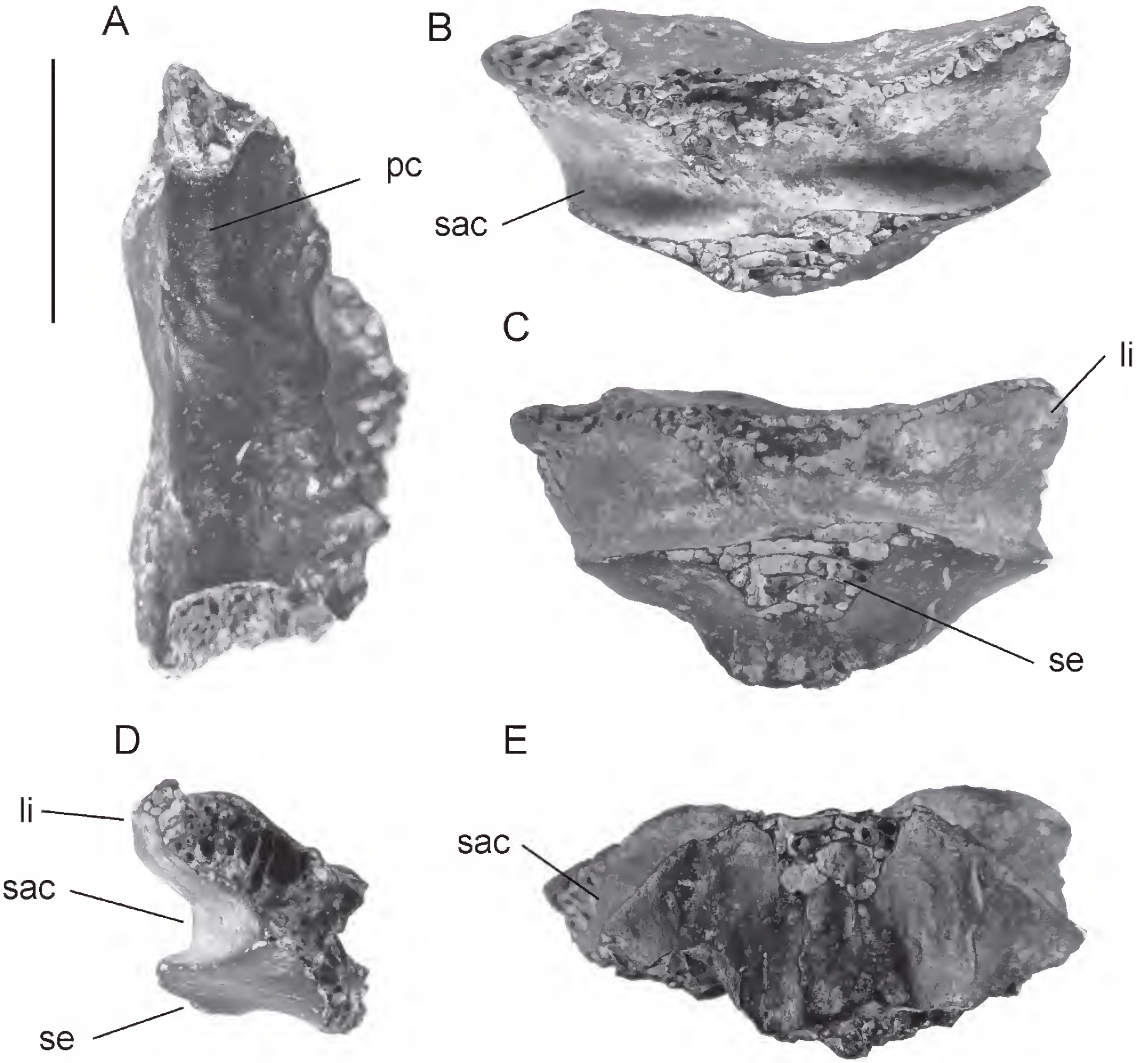

Figure 4. Views of NMNZ S.51257 in dorsal (A), cranial (B, C), left lateral (D), and ventral (E) views. Abbreviations: pc, pila coracoidea; sac, sulcus articularis coracoideus; li, labrum internum; se, base of spina externa. Scale bar = 1 cm.

(Anhingidae) and pelicans (Pelecanidae) are unknown from the fauna, despite their presence in the Oligo-Miocene of Australia (e.g., Boles, 2006). It is possible that these families may truly be absent from the St Bathans Fauna, but the recent discovery of *Palaelodus*, reported here, indicates that such a conclusion might well be premature. Instead, taphonomic limitations of the site may be a source of potential constraint on species representation and their numerical abundance. The St Bathans Fauna is derived from lacustrine fossil deposits that were laid down in shallow water in sandy—silty layers between layers of clay. Ripples in the sand layers reveal some wave action or water flow. Fossils are often concentrated on the down-flow side of shallow humps on the original lake bed and are also often found in the lee of larger objects like oncolites, adding further support to there having been a significant flow or current during the deposition of the beds. Further, there is complete disarticulation of all skeletons and most bones show variable wear consistent with erosion due to the tumbling action in the wave zone. Lastly, the fossil assemblage has higher proportions of elements that present least resistance to flow, e.g., carpometacarpi and coracoids. There are no entire pelves or sterna known and no fossil longer than 15 cm, even though fragments derive from some much larger bones. To summarize, these taphonomic biases result in all truly terrestrial taxa being very rare and bones larger than 15 cm absent, creating a marked bias against the discovery of identifiable fragments of all taxa larger than shelducks.

Waterfowl dominate the St Bathans assemblage and is explicable because ducks of the present day often aggregate in large flocks and so would be expected to dominate fossil deposits. Palaelodids can be very abundant in some deposits, with thousands of bones from St Gérand-le-Puy (Cheneval & Escuillié, 1992), suggesting that they too lived in flocks, but in South Australian deposits they occur as isolated specimens and are relatively rare with only one or two specimens per quarry or locality (Baird & Vickers-Rich, 1998; THW pers. obs., paleontology catalogue South Australian Museum).

Thus, the two, possibly three, specimens reported here from New Zealand of a medium-sized species of palaelodid suggest that it too probably lived in small numbers in paleo-Lake Manuherikia, not in the vast flocks flamingos can form. While we might expect truly terrestrial taxa, e.g., pigeons, owlet-nightjars to be rare in a lacustrine deposit (Worthy *et al.*, 2007), the fact that some waterbirds, e.g., a heron (Scofield *et al.*, 2010), is about as rare as the palaelodid, suggests that despite several thousand fossils documenting the avifauna, the current absence of the waterbirds listed above does not mean they were actually absent from the Miocene biota of Lake Manuherikia.

Despite these limitations, the developing St Bathans Fauna already reveals an avifauna with similarities to that of present day New Zealand and little in common with Oligo-Miocene Australia. There are no shared species, and as yet no casuariids, dromaiids, megapodiids, dromornithids, podicipedids, anhingids, phalacrocoracids, phoenicopterids, burhinids or cacatuids in the St Bathans Fauna, all of which have an Oligo-Miocene record in Australia (Boles, 2006; THW pers. obs.). The New Zealand waterfowl assemblage was dominated by oxyurines, as were waterfowl faunas in Australia and globally, and a tadornine was present as in Australian faunas, but all taxa differ at the generic level (Worthy *et al.*, 2007; Worthy & Lee, 2008; Worthy, 2009). Given the globally widespread distribution of *Palaelodus*, generic distinction of the New Zealand palaelodid would not be expected, but its specific distinction from Australian taxa is consistent with the endemicity of other New Zealand taxa.

The distinctiveness of the St Bathans Fauna can inform the debate on whether New Zealand was completely drowned during the Late Oligocene–Early Miocene 25–22 Ma (Pole, 1994; Gibbs, 2006; Heads, 2006; Waters & Craw, 2006; Campbell & Hutching, 2007; Trewick *et al.*, 2007; Landis *et al.*, 2008). While genetic studies of extant taxa are providing a growing body of data indicating that some diverged from sister taxa elsewhere long before the Oligocene highstand, for example hyriid molluscs (Graf & Foighil, 2000), freshwater crayfish (Apte *et al.*, 2007), anostostomatid orthopterans (Pratt *et al.*, 2008), geckoes (Chambers *et al.*, 2001), wattlebirds and stitchbirds (Driskell *et al.*, 2007; Shepherd & Lambert, 2007), kakapo and kaka (Tavares *et al.*, 2006), and kauri (Knapp *et al.*, 2007), only a fossil record can reveal what was actually present. The St Bathans Fauna has already revealed a number of taxa for which a vicariant origin is most likely, e.g., sphenodontids, leiopelmatid frogs, large flightless moa (Aves: Dinornithiformes), acanthisittid wrens, and an archaic stem terrestrial mammal (Worthy *et al.*, 2006, 2007, 2010; Jones *et al.*, 2009; Tennyson *et al.*, 2010). Some other taxa indicate a longevity in New Zealand of modern lineages since at least the Early Miocene, for example, anserines similar to *Cereopsis*, columbids of the *Hemiphaga* lineage, *Aegotheles, Pelecanoides* and diplodactyline geckoes, (Lee *et al.*, 2009; Worthy *et al.*, 2007, 2008, 2009). In addition, parrots, accipitrids, herons, shelducks and other waterfowl, rails and passerines including honeyeaters, while not known to be closely related to modern taxa, convey a distinctly New Zealand character to the fauna as a whole (Worthy *et al.*, 2007; Scofield *et al.*, 2010). Of those so far reported, only the swiftlet (*Collocalia*), cracticid songbirds and a crocodilian (Molnar & Pole, 1997; Worthy *et al.*, 2007) are representative of families no longer found in the New Zealand fauna, but Pleistocene and present cooler temperatures probably explain their absence. In short, all archetypical "New Zealand" endemic vertebrate taxa known from New Zealand in the Recent fauna are now know to have been present in the Early Miocene at a time perhaps no more than 3–4 Ma after maximal drowning of New Zealand. If New Zealand was completely submerged as Landis *et al.* (2008) contend, then all such taxa would need to have dispersed to New Zealand in this short period and no such taxa would have arrived in the subsequent 16 million years. Moreover, in some cases, e.g., leiopelmatids, sphenodontids, the recently discovered archaic mammal, and birds such as dinornithiforms, acanthisittids and aptornithids, there are no known source populations from which such dispersals could have emanated.

Our observations of the St Bathans Fauna, minimally some 3–4 million years after the maximal submergence, reveals a diverse fauna with little or no close relationship to the nearest up-wind land mass—Australia. Rather we see a mix, even then, of ancient endemics of Gondwanan origin and global influences such as members of the radiations of oxyurine anatids and palaelodids. In summary, the imperfect St Bathans Fauna already provides significant evidence of the persistence of taxa on Zealandia through the highstand, and minimally reveals a fauna whose general endemicity indicates that it had been evolving in isolation for millions of years. Given the limited depositional settings so far sampled and the brevity of investigations to date, compared to faunas such as those from Saint-Gérand-le-Puy and Sansan in France (Milne-Edwards, 1867–1871; Cheneval, 1983b, 1984), there will be many more first records yet for the St Bathans Fauna. Because this is the only fauna documenting the terrestrial vertebrate biota of New Zealand during the Tertiary, many first records representing novel lineages can be expected as increasingly more of New Zealand's Tertiary biota is documented for the first time.

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A Heron (Aves: Ardeidae) from the Early Miocene St Bathans Fauna of Southern New Zealand

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ABSTRACT. We describe a fossil heron, based on seven fossil bones, from the Early Miocene Bannockburn Formation at Saint Bathans, Central Otago in the south of New Zealand. Based on a phylogenetic analysis of 50 morphological characters, we determine the new heron is a member of Ardeidae but, in an analysis where we retrieve three major lineages in Ardeidae: (1) bitterns, (2) egrets and true herons, and (3) night herons, there is no support for a sister group relationship with any of these clades. We discuss aspects of the higher taxonomy of the herons based on our phylogeny.

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The herons (Aves: Ardeidae) are a cosmopolitan group, found on all continents except Antarctica. The group's fossil record may extend back as far as the Eocene (Table 1 and references therein), however, analyses to date of the fossil taxa are not informative of their intrafamilial phylogenetic relationships. The Recent herons are currently divided into five subfamilies (Kushlan & Hancock, 2005; Table 2). Ardeinae and Botaurinae have a fossil record extending into the Miocene; the Tigrisomatinae's only fossil occurrence is in the Pleistocene of the West-Indies (see Table 1 and references therein); and there are no fossil records for Argaminae or Cochleariinae. Here we describe a fossil heron based on seven fossil bones, from the Early Miocene Saint Bathans Fauna of New Zealand.

Geological setting and St Bathans Fauna

The St Bathans Fauna, of late Early Miocene age, Altonian, 19–16 Ma, is derived from the lower Bannockburn Formation of the Manuherikia Group, in Otago, South Island, New Zealand (Worthy *et al.*, 2007). The sediments were deposited in a shallow freshwater lake, about 5600 km^2 in area, in a warm climate, with a surrounding vegetation including casuarinas (Casuarinaceae), eucalypts (Eucalyptus: Myrtaceae) and palms (Arecaceae), in addition to the typical New Zealand podocarps (Podocarpaceae), *Nothofagus* and araucarias (Araucariaceae) (Pole & Douglas, 1998; Pole *et al.*, 2003). The diverse fauna provides the only data on the terrestrial vertebrates existing in New Zealand during the

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Table 1. The fossil record of the Ardeidae.

taxon [a]	age	location	reference	notes
Ardeid subfamily indeterminate [or undetermined]				
Ardeidae sp	Eocene	Washington State, USA	(Mustoe, 2002)	Based on fossil footprints
Ardea piveteaui	Upper Eocene	Montmartre, France	(Brunet, 1970; Cracraft, 1971)	Specimen considered too fragmentary—should simply be ardeid sp. (Cracraft, 1971)
Calcardea junnei	Lower Eocene	Wyoming, USA	(Gingerich, 1987)	
Eoceornis ardetta	Middle Eocene	Wyoming, USA	(Shufeldt, 1915)	
Ardeagrandis arborea	Late Miocene	Golboçica, Moldova	(Kuročkin & Ganea, 1972)	
?*Ardea alba*	Miocene	Abu Dhabi	(Harrison, 1979)	Specimen considered too fragmentary—should simply be ardeid sp. (Stewart & Beech, 2006)
Ardeinae				
Proardea amissa (synonyms are *Proardeola walkeri* and *Ardea aurelianensis*)	?Late Eocene-Late Oligocene-Miocene	France	(Milne-Edwards, 1892; Lambrecht, 1933)	Synonymy *fide* C. Mourer-Chauviré (Olson, 1985: 167; Mlíkovský, 2002)
Ardea basaltica (synonym is *Anas basaltica*)	Lower Oligocene	Czech Republic	(Bayer, 1882)	Synonymy *fide* Mlíkovský & Švec (1989)
Ardea sp.	Mid-Miocene	Nebraska, USA	(Becker, 1986)	
Egretta subfluvia	Late Miocene or Early Pliocene	Florida, USA	(Becker, 1985)	
Ardea polkensis	Early Pliocene	Florida, USA	(Brodkorb, 1955)	
Ardea howardae	Plio / Pleistocene	Ethiopia	(Brodkorb, 1980)	
Butorides validipes	Late Pliocene	Florida, USA	(Campbell, 1976)	
Nycticoracinae [sensu Payne & Risley (1976)]				
Nycticorax sp.	Early Oligocene	Egypt	(Rasmussen *et al.*, 1987)	
Zeltornis ginsburgi	Miocene	Libya	(Balouet, 1981)	
Nycticorax sp.	Miocene	Kenya	(Dyke & Walker, 2008)	
Botaurinae				
Palaeophoyx columbiana	Upper Pleistocene	Florida, USA	(McCoy, 1963)	Originally referred to Ardeinae but synonymized with extant *Botaurus lentiginosus* by Olson (1974)
Tigrisomatinae				
Tigrisoma mexicanum	Pleistocene	Cuba	(Olson & Suarez 2008)	
taxa no longer considered herons				
Proherodius oweni			(Lydekker, 1891)	Now considered Aves *incertae sedis*, because of the lack of diagnostic characters in the existing material (Dyke, 2001)
Botauroides parvus			(Shufeldt, 1915)	Transferred to the Primobucconidae by Feduccia (1996) and to the Sandcoleidae by Houde & Olson (1992)
Xenerodiops mycter	Early Oligocene	Eygpt	(Rasmussen *et al.*, 1987)	Originally placed in a new family Xenerodiopidae but this was synonymized into Nycticoracinae by Mlíkovský (Olson, 1985; Mlíkovský, 2002; Mlíkovský, 2003). G. Mayr (2009) considers this to differ from extant ardeids in a number of features and placed it as *incertae sedis*
Calcardea junnei	Lower Eocene	Wyoming, USA	(Gingerich, 1987)	G. Mayr (2009) considers this to differ from extant ardeids in a number of features and placed it as *incertae sedis*.

[a] Nomenclature as originally described.

entire Tertiary and includes a crocodylian, a sphenodontid, squamates, at least 30 taxa of birds, several bats and an archaic terrestrial mammal (Molnar & Pole, 1997; Worthy *et al.*, 2006; Hand *et al.*, 2007; Worthy *et al.*, 2007; Worthy & Lee, 2008; Worthy *et al.*, 2008; Jones *et al.*, 2009). In addition, undescribed terrestrial and freshwater molluscs are diverse (unpubl. data), and fish are abundant (McDowall & Pole, 1997; McDowall *et al.*, 2006; Lee *et al.*, 2007).

The avifauna of the St Bathans Fauna is dominated by anseriforms, with a minimum of eight taxa in five genera, but the fauna also includes procellariiforms, accipitriforms, gruiforms, charadriiforms, columbiforms, psittaciforms, apodiforms, and passeriforms (Worthy *et al.*, 2007; Worthy & Lee, 2008; Worthy *et al.*, 2010).

The St Bathans avifauna is known from exposures along the Manuherikia River and at several other nearby sites (see Worthy *et al.*, 2007 for location data). The fossils described here derive from three discrete layers (HH1a, HH1b and HH4) in the Manuherikia River Section. These layers are poorly aged but considered to be late Early Miocene age, 19–16 Ma. It is not known what temporal period they represent nor the interval between them. They have revealed thousands of avian fossils, but the seven fossils described here are the only heron remains identified to date.

The primary layer (HH1a; NZFRN H41/f0088) is 6.88–7.00 m above the base of the Bannockburn Formation. It is mostly greenish gray fine sand, sometimes intermixed with quartz granules/pebbles, and organic debris, incorporating carbonate-encrusted mud rip-up clasts and rare oncolite fragments derived from algal growth and abundant bone fragments. In the HH1a strata, most of the heron fossils come from an excavated pit extending approximately 20–40 m from the current riverbank. A single element (the mandible tip) comes from a trench 60 m inland from the riverbank in a layer (HH1b; NZFRN H41/f0103) which is 9.5–9.58 m above base of the Bannockburn Formation. The third stratum (HH4; NZFRN H41/f0096) was a discrete lens, up to 5–15 cm thick, in a clay layer exposed 20 m downstream from HH1a in the riverbank itself and is 25.63–25.83 m above the base of the Bannockburn Formation. This lens was completely quarried away in 2008 and was characterized by abundant fragments of the freshwater gastropod *Glyptophysa*, but it also contained terrestrial vertebrate remains.

Materials and methods

Institutional abbreviations. AM, Australian Museum, Sydney, Australia; CM, Canterbury Museum, Christchurch, New Zealand; MV, Museum Victoria, Melbourne, Australia; NMNZ, Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand; SAM, South Australian Museum, Adelaide, South Australia, Australia; UMMZ, University of Michigan Museum of Zoology, Michigan, United States of America; NMNH, National Museum of Natural History, Washington, D.C., United States of America.

Anatomical nomenclature. Names for specific bone landmarks follow Baumel & Witmer (1993) with English translations of less specific areas on each element following Howard (1929). Here we use the terms plantar and dorsal rather posterior and anterior to describe positions on the tarsometatarsus following Baumel & Witmer (1993). For the nomenclature of the hypotarsal canals we follow Strauch (1978). Nomenclature of the avian quadrate follows Elzanowski *et al.* (2000). Some common terms are abbreviated as follows: *L*, left; *R*, right; *lig*, ligamentum; *tuber*, tuberculum; *Ma*, million years ago; *indet*, indeterminate. Other abbreviations follow Baumel & Witmer (1993). Anatomical landmarks are abbreviated in figure captions.

Table 2. Recent and extant nomenclature of the family Ardeidae based on the nomenclature of Kushlan & Hancock (2005).

subfamilies	tribes	genera	common name
Tigrisomatinae		*Tigrisoma*	Tiger herons
		Tigriornis	
		Zonerodius	
Agaminae		*Agamia*	Agami heron
Cochleariinae		*Cochlearius*	Boat-billed heron
Ardeinae	Ardeini	*Ardeola*	Day herons
		Butorides	
		Ardea	
	Egrettini	*Egretta*	Egrets
		Nyctanassa	
		Pilherodius	
		Syrigma	
	Nycticoracini	*Nycticorax*	Night herons
		Gorsachius	
Botaurinae		*Zebrilus*	Bitterns
		Ixobrychus	
		Botaurus	

Comparative material (Some features were scored from illustrations in Payne & Risley [1976]. In these cases the registration numbers of the specimens used in these illustrations are given in square brackets). The generic and species level taxonomy of the ardeids is complex and many issues are unresolved—here we follow Kushlan & Hancock (2005).

Ciconiiformes Bonaparte, 1854

Ardeidae Leach, 1820: Ardeinae Leach, 1820: *Ardea herodias* (Linnaeus, 1758), Great Blue Heron, CM Av19902; *Ardea goliath* Cretzschmar, 1829, Goliath Heron, CM Av7120; *Ardea modesta* J.E. Gray, 1831, Eastern Great Egret, CM Av 16554, CM Av 22663, CM Av 26515, CM Av36581, CM Av36585, CM Av36587, CM Av36590; *Ardea ibis* Linnaeus, 1758, Cattle Egret CM Av 29417 [NMNH 430524, NMNH 430525, UMMZ 209241]; *Egretta rufescens* (Gmelin, 1789), Reddish Heron [UMMZ 136370]; *Egretta novaehollandiae* (Latham, 1790), White-faced Heron, CM Av 5215, CM Av 14806, CM Av 25210; Whistling Heron, [UMMZ 158606, 158607]; *Nycticorax caledonicus* (Gmelin, 1789), Nankeen Night Heron, NMNZ OR.19310; SAM B.48523; *Nyctanassa violacea* (Linnaeus, 1758), Yellow-crowned Night Heron, [UMMZ 85046, UMMZ 130935, UMMZ 133607]; *Pilherodius pileatus* (Boddaert, 1783), Capped Heron, [UMMZ 156863].

Tigrisomatinae Bock, 1956: *Tigrisoma mexicanum* Swainson, 1834, Fasciated Tiger Heron, MV B13558; *Syrigma sibilatrix*, (Temminck, 1824).

Botaurinae Reichenbach, 1850: *Botaurus lentiginosus* (Rackett, 1813), American Bittern, CM Av 19627; *Botaurus poiciloptilus* (Wagler, 1827), Australasian Bittern, CM Av 5085, CM Av 5085, CM Av 5502; *Ixobrychus sinensis*

(Gmelin, 1789), Yellow Bittern, [NMNH 291696, 488913]; *Ixobrychus minutus* (Linnaeus, 1766), Little Bittern, CM Av 7122, [UMMZ 151097].

Cochleariinae Chenu & Des Murs, 1854: *Cochlearius cochlearius* (Linnaeus 1766), Boat-billed Heron, CM Av 39999.

Scopidae Bonaparte, 1849: *Scopus umbretta* Gmelin, 1789, Hamerkop, CM Av 39998.

Balaenicipitidae Bonaparte, 1853: *Balaeniceps rex* Gould, 1850, Shoebill, [UMMZ 215884].

Ciconiidae Sundevall, 1836: *Ciconia ciconia* (Linnaeus, 1758), White Stork, CM Av 33450.

Threskiornithidae Poche, 1904: *Threskiornis molucca* Cuvier, 1829, Australian White Ibis, CM Av 16219; *Plegadis falcinellus* Linnaeus, 1766, Glossy Ibis, CM Av 20692.

Pelecaniformes Sharpe, 1891

Phalacrocoracidae Reichenbach, 1850: *Phalacrocorax carbo* (Linnaeus, 1758), Black Shag, CM Av 17299.

Phoenicopteriformes Fürbringer, 1888

Phoenicopteridae Bonaparte, 1831: *Phoenicopterus ruber* Linnaeus, 1758, American Flamingo, CM Av 7113.

Determining if all bones are from the same species. In order to determine whether all the elements described here are from the same medium-sized heron an intra-element ratio comparison of elements was made using Simpson's ratio-diagrams (Simpson, 1941).

Phylogenetic analyses

The phylogenetic analyses were aimed principally at determining the relationships of the fossil heron bones from the St Bathans Fauna. They were thus mainly constrained to the use of characters derived from the available elements: the tarsometatarsus; the cranial end of a coracoid; a quadrate; an axis vertebra; and a tip of a mandible. In the present analyses, 24 terminal taxa were included. Six taxa were defined as the outgroup: five Ciconiiformes—*Balaeniceps rex, Ciconia ciconia, Threskiornis molucca, Plegadis falcinellus*, a flamingo *Phoenicopterus ruber* and a pelecaniform *Phalacrocorax carbo*. The sister taxon to ardeids is unknown, but is usually considered to be a member of the Ciconiiformes. The details of this relationship, however, are poorly understood. For example, using a significant number of DNA loci, Hackett *et al*. (2008) found the Threskiornithidae to form a clade with the ardeids, with other Ciconiiformes as their sister group, but Livezey & Zusi (2007), using a large morphological dataset considered the Ardeidae to form their own order, the Ardeiformes, and to be the sister group to all other Ciconiiformes including Threskiornithidae. To take into account this uncertainty, we sampled a wide variety of Ciconiiformes. We sampled all four extant resident Recent New Zealand species of ardeids: *Ardea novaehollandiae; Ardea modesta*; *Botaurus poiciloptilus* and *Nycticorax caledonicus* and species from two of the three extralimital ardeid subfamilies (see *Comparative material*).

By comparing the fossil elements with specimens of Recent ardeids we defined a set of characters (Appendix 1), which were scored for all taxa (Appendix 2). Many are new characters, although some derive from features described by others (e.g., Strauch, 1978; Livezey & Zusi, 2007). Missing data was identified as either: (1) Inapplicable characters (coded as "—"), which could not be objectively scored in a particular taxon due to extensive divergence obscuring homology, or (2) Unknown characters (coded as ?) which were not preserved in the specimens examined. We scored features of the proximal tarsometatarsus despite it not being represented in the fossil material, so as to increase the numbers of characters and improve resolution of compared taxa. The phylogenetic analyses used PAUP* 4.0b10 (Swofford, 2002). While distinguished in our matrix (Appendix 2), PAUP treats both types of missing data in the same fashion.

Parsimony analyses used heuristic searches with tree-bisection-reconnection (TBR) branch swapping, and 1,000 random addition replicates per search. Trees were rooted with the outgroup forming a polytomy at the base of the tree. When calculating tree lengths, multistate taxa were treated as polymorphisms rather than ambiguity. Bootstrapping used heuristic searches and the same options. Strict consensus trees were computed and presented. Trees were manipulated and labelled in MrEnt (Zuccon & Zuccon, 2008).

Bayesian analyses

The program MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003) was used to determine posterior probabilities for clades in the tree. The analyses were performed with the same characters and ordering assumptions as above; however, the outgroup was restricted to *Phalacrocorax carbo* as multiple outgroups are not allowed.

The following priors were used. Characters were assumed to have rate variability distributed according to gamma parameter (rates = gamma) with flat prior distribution (0–200). In the morphological data set, only variable characters were assumed to have been included (coding = variable).

Two independent analyses were run simultaneously to check for adequacy of convergence, each for 5,000,000 generations, sampled every 1,000 generations. To improve exploration of tree topology space, the heating parameter was set to 0.20, six chains (one cold and five incrementally-heated) per analysis were used, and branch swapping was set at three times the default (nswaps = 3). The time to convergence for topology, stationarity, and all parameters was checked using Tracer v. 1.3 (Rambaut & Drummond, 2004); the first 1,000 sampled trees were discarded as burnin. A standard "all-compat" consensus tree, where all clades are shown regardless of posterior probabilities values, was produced by combining the post-burnin 4001 samples from each run. Posterior probability values for a node are the percentage of sampled generations that have that node.

Systematic paleontology

Order Ciconiiformes Bonaparte, 1854

Family Ardeidae Leach, 1820

The fossils are referred to the Ardeidae using characteristics of the tarsometatarsus and coracoid.

The tarsometatarsi (NMNZ S.50003 and S.51264) can be distinguished from other Aves by the combination of the following characters (based on Brodkorb, 1980 and pers. obs.):

1. Shaft long, narrow, wider than deep, narrowest just proximal of base of trochlea metatarsi II;
2. Hypotarsal ridges (crista hypotarsus) extends considerably less than ½ the length of the shaft;
3. Trochlea metatarsi II and III extend about the same distance distally;
4. Absence of a sulcus flexorius;
5. A distinct raised facet for the articulation of metatarsal I rather than a sulcus;
6. Trochlea metatarsi II–IV roughly in the same dorso-plantar plane;
7. No medial inflection in trochlea metatarsi II or lateral deflection in trochlea metatarsi IV.

In addition, herons are typified by a single small closed tendinal canal (canalis hypotarsi) and a single distinct hypotarsal ridge (crista hypotarsi), both not preserved in the available material.

The cranial extremity of the coracoid (NMNZ S.50004) can be diagnosed as an ardeid by the combination of the following characters (based on Brodkorb, 1980; Gilbert *et al.*, 1981 and pers. obs.):

1. Brachial tuberosity (tuber. brachiale) present;
2. Raised oval humeral facet (facies artic. humeralis) faces dorsally;
3. Absence of a deep groove running along the medial face between the brachial tuberosity and the tip of the procoracoid (proc. procoracoideus);
4. Relatively small hook-shaped procoracoid bent slightly medially;
5. Distance between scapular facet (cotyla scapularis) and cranial most end of acrocoracoid (proc. acrocoracoideus) approximately equal to width of shaft at the procoracoid;
6. Scapular facet, raised and flattened but not cup-like.

Matuku n.gen.

Type species. *Matuku otagoense* n.sp.

Diagnosis. Tarsometatarsus shaft relatively short and robust: trochlea metatarsi II with slight medial deflection; trochlea metatarsi III in line with axis of shaft; trochlea metatarsi IV deeply grooved distally; foramen vasculare distalis with dorsal opening distinct from intertrochlear incision and large; and crista planataris medialis dorso plantarly thick. The coracoid is distinguished by three autapomorphies:

1. the extremely short distance from the cranial side of the clavicular facet (facies articularis clavicularis) to the omal tip of the facet;
2. a broad triangular (impressio ligamentum acrocoracohumeralis), rather than the rectilinear impression normally seen in herons;
3. the clavicle facet (facies clavicularis) on the acrocoracoid (proc. acrocoracoideus) overhangs the supracoracoidal sulcus as a prominent lip, rather than the acrocoracoid being in line with the medial margin of the sulcus.

Etymology. *Matuku* is the New Zealand Māori word for a heron. As the name ends in a “u” it is treated as neuter as specified by Article 30.2.4 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 1999).

Matuku otagoense n.sp.

Holotype. NMNZ S.50003: Distal end, shaft and lateral proximal edge of left tarsometatarsus with fragmentary lateral cotyla and basal hypotarsus; the three trochlea are preserved but the distal foramen is obscured; the medial proximal end is missing. The bone was already fragmented *in situ* when discovered and has subsequently been repaired in the laboratory (Figs 1, 2). It was collected on 9 January 2007 during a University New South Wales, NSW, Australia/University of Adelaide, South Australia/Canterbury Museum, Christchurch, NZ/Museum of New Zealand Te Papa Tongarewa, Wellington, NZ, expedition.

Diagnosis. As for genus.

Etymology *otagoense*, Latin, after Otago province in southern New Zealand, where the excavations take place; gender neuter, conforming to the gender of the generic name.

Type locality. Home Hills Station, Site HH4, true left side Manuherikia River, Otago, New Zealand. 44° 54.472'S 169° 51.434'E. NZMS 260 H41/618843, New Zealand Fossil Record File Number H41/f0095. The site was first exposed by river erosion between February 2005 and March 2006. Bones were recovered from the site in March 2006 and January 2007.

Stratigraphy/Age/Fauna. Bannockburn Formation, Manuherikia Group, Early Miocene (Altonian); 19–16 Ma; St Bathans Fauna. HH4 is a 5–15 cm thick clay-silt layer notable for the large number of shell fragments of the gastropod *Glyptophysa*. It is located 2.15–2.35 m above the top of an obvious oncolite layer and 25.63–25.83 m above base of Bannockburn Formation.

Measurements of holotype. See Table 3.

Paratypes. NMNZ S.51264. Distal end of tarsometatarsus, missing distal end of all three trochlea (HH1b Trench excavation, 15 January 2008); NMNZ S.50004. Cranial end of right coracoid, broken approximately half way down shaft (HH1a, 8 January 2007); NMNZ S.50852. Left quadrate missing entire proc. orbitalis (HH4, 8–16 January 2008); NMNZ S.50854. Left quadrate missing entire proc. orbitalis (HH1a, 15 January 2008); NMNZ S.50853. Axis with damage to caudal end of proc. caudalis (HH4, 8–16 January 2008); NMNZ S.51174. Tip of mandible including most of mandibular symphysis, but with damage to tip (HH1b trench excavation, 14 January 2008).

Tarsometatarsus (NMNZ S.51264, not illustrated).

In its exterior appearance, this fragmentary element does not differ significantly in any way from NMNZ S.50003. The exceptional preservation of the distal foramen in this specimen, however, allows us to see a feature that can not be discerned in NMNZ S.50003. In NMNZ S.51264, the dorsal opening of the foramen does not open into the inter-

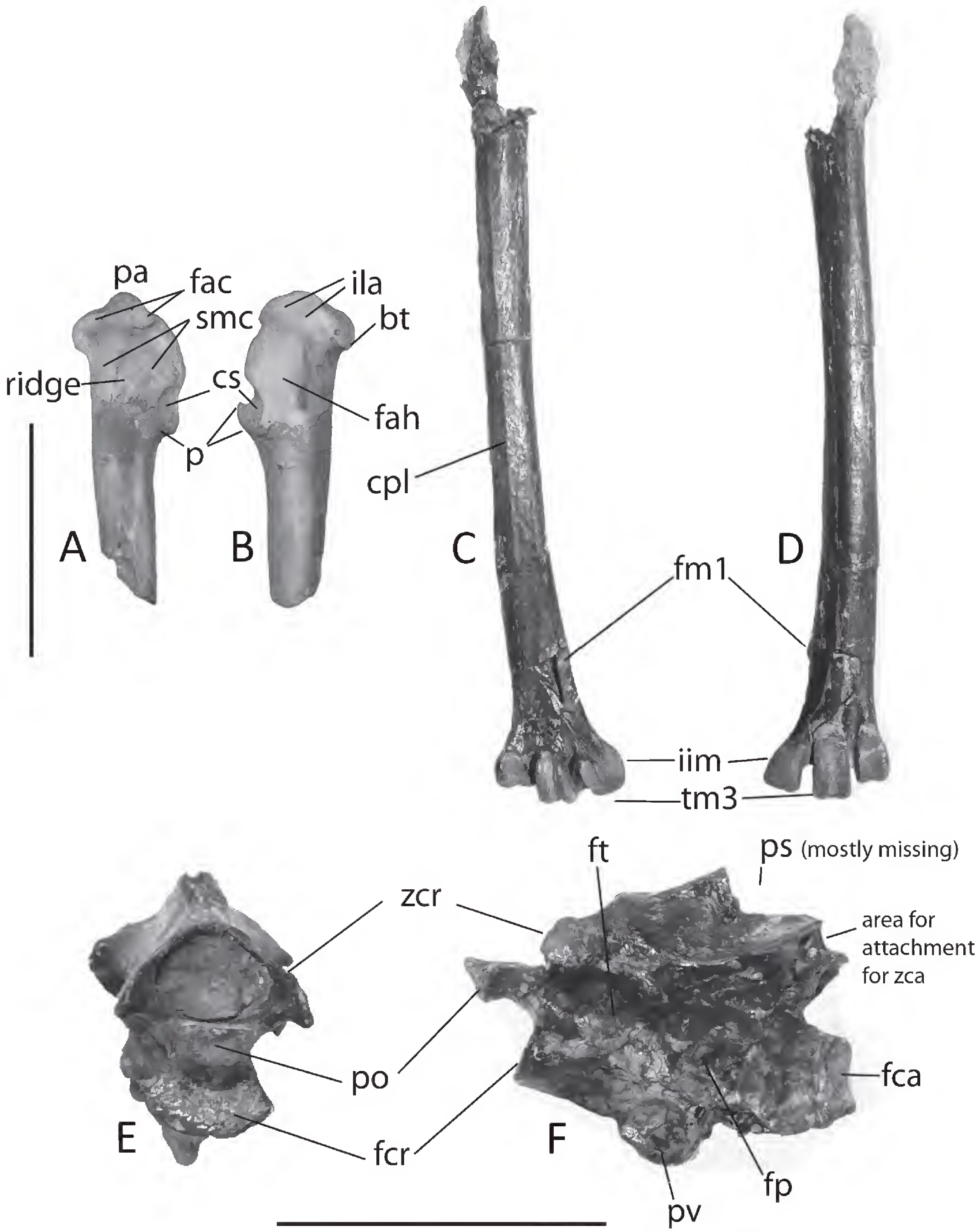

Figure 1. Specimens of the fossil heron *Matuku otagoense*. Scale bar is 1 cm. Right coracoid, extremitas omalis, paratype of *Matuku otagoense*, S.50004, HH1a, in medial (*A*) and lateral (*B*) aspects; left tarsometatarsus, holotype of *Matuku otagoense*, S.50003, HH4, in plantar (*C*) and dorsal (*D*) aspects; and referred axis vertebra S.50853, HH4, in cranial (*E*) and left lateral (*F*) aspects. Abbreviations: **fac**, clavicular facet, *facies articularis clavicularis*; **smc**, supracoracoidal sulcus, *sulcus musculi supracoracoidei*; **ridge**, character 23 "Slight ridge running sternally, barely dividing sulcus into two segments"; **pa**, acrocoracoid, *processus acrocoracoideus*; **fah**, humeral facet, *facies artic. humeralis*; **ila**, impression for the acrocoracohumeralis ligament, *impressio ligamentum acrocoracohumeralis*; **bt**, brachial tuberosity; **p**, procoracoid, *proc. procoracoideus*; **cpl**, *crista plantaris lateralis*; **fm1**, *fossa metatarsal I*; **imm**, *Incisura intertrochlearis medialis*; **tm3**, *trochlea metatarsi III*; **po**, dens, *processus odontoideus*; **fcr**, cranial facies of articulation, *facies articularis cranialis*; **zcr**, prezygapophysis, zygapophysis cranialis; **fca**, caudal facies of articulation, *facies artic. caudalis*; **zca**, postzygapophysis, zygapophysis caudalis; **pv**, hypapophysis, *proc. ventralis corporis*; **fp**, pneumatic foramen, *foramen pneumaticum*; **ps**, spinous process, *proc. spinosus*; **ft**, transverse foramen, *foramen tranversarium*.

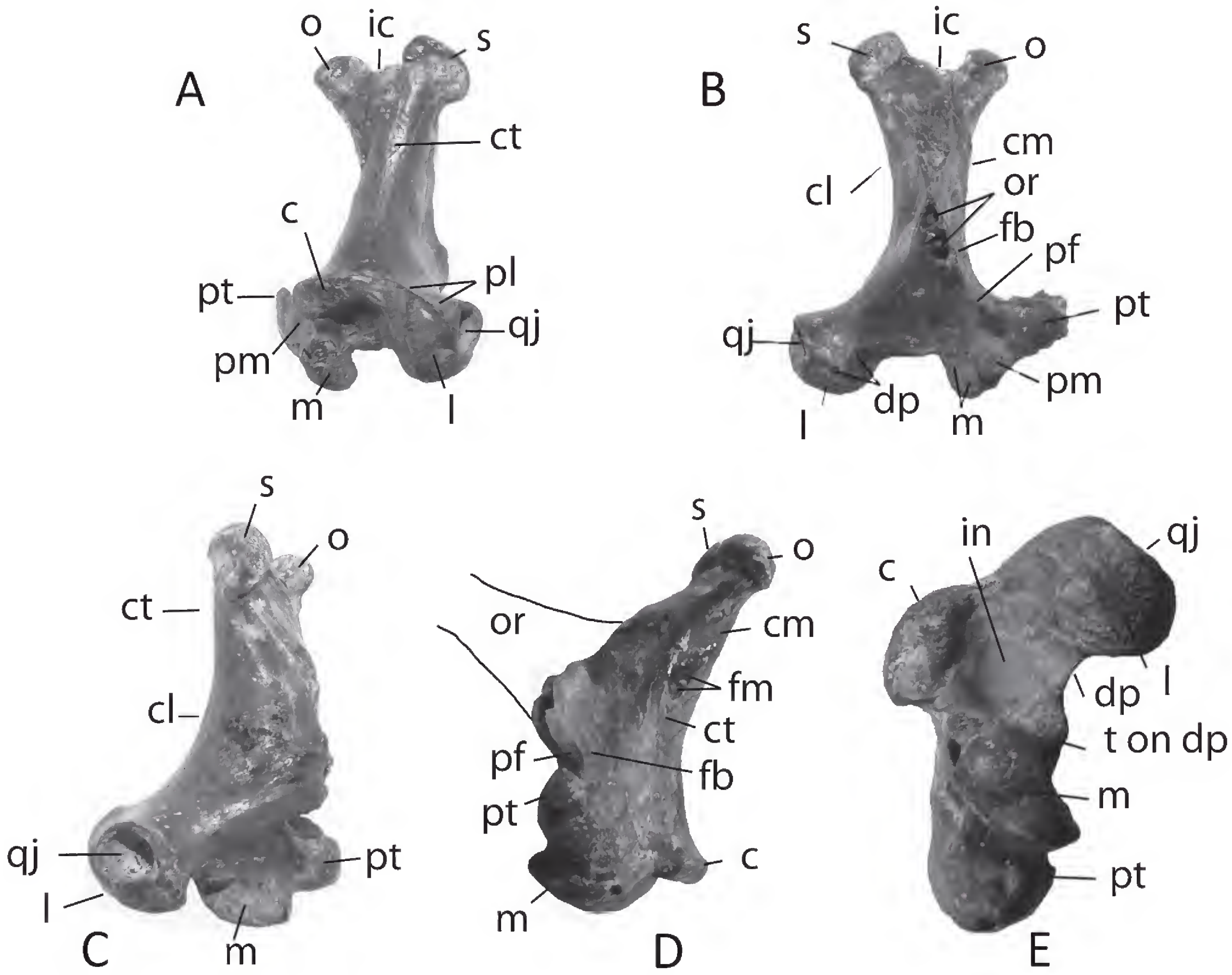

Figure 2. Referred specimens of the fossil heron *Matuku otagoense*. Scale bar is 1 cm. Left quadrate (S. 50852; HH4): (*A*) caudal aspect; (*B*) rostral aspect; (*C*) lateral aspect; (*D*) medial aspect; (*E*) ventral aspect. Abbreviations: **o**, *capitulum oticum*; **ic**, *vallecula intercapitularis*; **s**, *capitulum squamosum*; **ct**, *crista tympanica*; **c**, *condylus caudalis*; **pt**, *condylus pterygoideus*; **pm**, *processus medialis*; **m**, *condylus medialis*; **l**, *condylus lateralis*; **pl**, *processus lateralis*; **cm**, *crista medialis*; **cl**, *crista lateralis*; **or**, *processus orbitalis*; **fb**, *fossa basiorbitalis*; **pf**, *facies pterygoidea*; **dp**, *depression praecondylaris*; **qj**, *cotyla quadratojugalis*; **fm**, *foramen pneumaticum mediale*; **in**, vallecula intercondylaris; **t on dp**, tubercle on *depressio praecondylaris*.

trochlear incision but is separated from it, by a thin lamella giving the foramen three openings, one dorsally, one opening to the incision and one plantarly. This feature appears to be a feature the fossil shares only with *Syrigma* and *Botaurus* amongst the ardeids examined.

Differential diagnosis of tarsometatarsi

Subfamily Ardeinae
(Day Herons, Egrets, Night Herons)

Support for the inclusion of *Matuku* in Ardeidae is provided by a single unambiguous apomorphy: the absence of a plantar metatarsal groove (*sulcus flexorius*) and coincident presence of metatarsal facet. The tarsometatarsi of night herons (tribe Nycticoracini) differ from those of other members of the Ardeidae, by the following combination of characters (Steadman *et al.*, 2000):

1 The trochlea metatarsi IV is slightly grooved distally, rather than deeply grooved or ungrooved.
2 The distal foramen (foramen vasculare distale) is small and placed more proximally than the proximal end of trochlea metatarsi III.
3 The trochlea metatarsi III is deflected laterally from the axis of the shaft (corpus tarsometatarsi) in night herons (this character is shared only with bitterns).
4 The trochlea metatarsi II has slight deflection from the shaft (corpus tarsometatarsi) so extends only slightly mesad of the shaft, not markedly.
5 The crista plantaris medialis is prominent proximally.
6 There is a lack of obvious dorsal metatarsal (sulcus extensorius) and plantar metatarsal grooves (sulcus flexorius) with the crista plantaris lateralis being indistinct.

Matuku otagoense differs from members of Nycticoracini in all these features and most noticeably in the lack of lateral deflection of trochlea metatarsi III and in having a large distal foramen. Additionally, members of this tribe have the medial margin of the shaft immediately distal to the cotyla medialis dorso-plantarly compressed forming a prominent thin crest, which *Matuku otagoense* lacks.

Tarsometatarsi of day herons and egrets (Tribes Ardeini and Egrettini respectively) have obvious dorsal metatarsal and plantar metatarsal grooves, with a distinct

Table 3. Measurements of *Matuku otagoense*. Alphabetical notation given is used in Fig. 4. NMNZ S.51264 and S.51174 were not measured due to their fragmentary nature.

abbreviation	description	mm
tarsometatarsus (holotype S.50003)		
A	maximum distal width	12.9
B	maximum distal depth	7.9
C	width of trochlea metatarsi III	3.8
	preserved length	92.6
D	estimated total length	ca. 98
right coracoid (S.50004)		
E	maximum cranial width (from humeral facet to brachial tuberosity)	8.0
F	maximum shaft width (below procoracoid)	5.4
G	length of humeral facet	8.3
H	depth of humeral facet	5.7
left quadrate (S.50852)		
I	depth from capital squamosum to cond. lateralis	16.9
J	depth from capital squamosum to cond. medialis	16.9
left quadrate (S.50854)		
I	depth from capital squamosum to cond. lateralis	16.8
J	depth from capital squamosum to cond. medialis	16.9
axis (S.50853)		
K	width of facies artic. cranialis	4.1
L	inter condyle distance	13.6
M	width single zygapophysis caudalis	3.6
N	depth single zygapophysis caudalis	3.6
O	greatest width (estimated across zygapophyses caudalis)	10.3

lateral intermuscular line (crista plantaris lateralis). The tarsometatarsi of *Egretta* and most *Ardea* are much longer with comparatively narrower shafts than *Matuku otagoense*, but those of *Butoroides* and *Ardea ibis* are shorter and more gracile than the fossil. We conclude therefore, that the St Bathans fossil is not an ardein heron.

Subfamily Cochleariinae (Boat-billed Herons)

The tarsometatarsus of *Cochlearius* (Cochlearinae) is very similar to that of *Nycticorax* but differs in the following characters: in *Cochlearius* the dorsal metatarsal groove is slightly deeper and usually more well defined; the intercotylar prominence usually projects less proximally; the trochlea metatarsi III is less elevated relative to the trochlea metatarsi IV; the trochlea metatarsi II is less wide. None of these features are found in *Matuku otagoense*.

Subfamily Botaurinae (Bitterns)

The tarsometatarsi of bitterns have a prominent plantar metatarsal groove (sulcus flexorius) with a prominent central intermuscular line (crista plantaris), quite unlike the flatter morphology of *Matuku otagoense*. Also, the trochlea metatarsi III is deflected laterally from the shaft axis and they have a very small or lack a distal foramen.

Subfamily Tigrisomatinae (Tiger herons)

The tarsometatarsi of tiger herons differs from *Matuku otagoense* in the more proximal position of dorsal opening of the distal foramen relative to the proximal end of trochlea metatarsi III (equal in *Matuku*), the significant medial protrusion of trochlea metatarsi II from the shaft (weak in Matuku), and the weak crista plantaris lateralis (strong in *Matuku*).

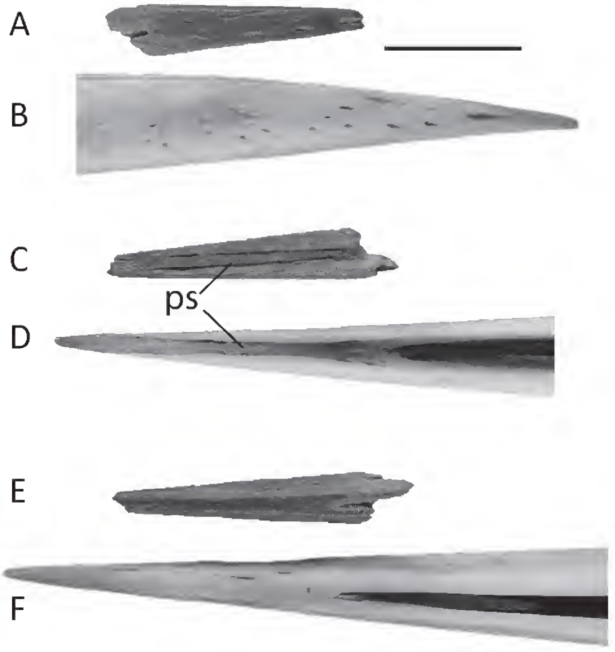

Figure 3. Mandible tips of referred specimen of the fossil heron *Matuku otagoense* n.sp., (S.51174, HH1a), (*A, C, E*) and Recent Nankeen Night Heron *Nycticorax caledonicus*, SAM B.48523, South Australia, (*B, D, F*). Scale bar is 1 cm. Rostrum mandibulae: in medial aspect (*A, B*); in dorsal aspect (*C, D*), and in ventral aspect (*E, F*) ventral aspect. Abbreviation: *ps*, *pars symphysialis.*

Subfamily Agaminae (Agami Heron)

Although not examined by us, the skeleton of *Agamia* is said to differ little in morphology from the Ardeini and Egrettini (Payne & Risley, 1976).

Coracoid (Fig. 2). The fossil coracoid most closely matches that of *Cochlearius*. The three autapomorphies on the coracoid (see diagnosis of *Matuku* above) justify the placement of *Matuku otagoense* outside the five traditional subfamilies of Ardeidae.

Quadrates (S.50852, Fig. 2; S.50854, not illustrated)

The two quadrates are typical ardeid quadrates. In overall proportions and morphology they are most similar to *Cochlearius* but differ in lacking a large foramen pneumaticum mediale. These quadrates, that we refer to *Matuku,* are distinguished by one autapomorphy from all living species of the Ardeidae examined: in ventral aspect the vallecula intercondylaris is a deep "U" shaped fossa, opening into a wide sulcus on the rostral surface.

Axis (Fig. 1). The axis does not differ significantly from some extant members of the Egrettini and Ardeini, although the knob-like protruding hypapophysis (*processus ventralis corporis*) is more similar to *Cochlearius*. However, *Matuku* differs from *Cochlearius* in relative proportions. The axis of *Matuku* is not as elongate as it is in *Ardea* and *Egretta*, nor so short and robust as it is in *Nycticorax*.

Mandible tip (Fig. 3). The mandible tip referred to *Matuku* is most similar in proportions to that of *Nycticorax*, with the symphysis much shorter than it is in *Egretta* or *Ardea.* A mandible of this type suggests a bill designed for the stabbing capture of prey.

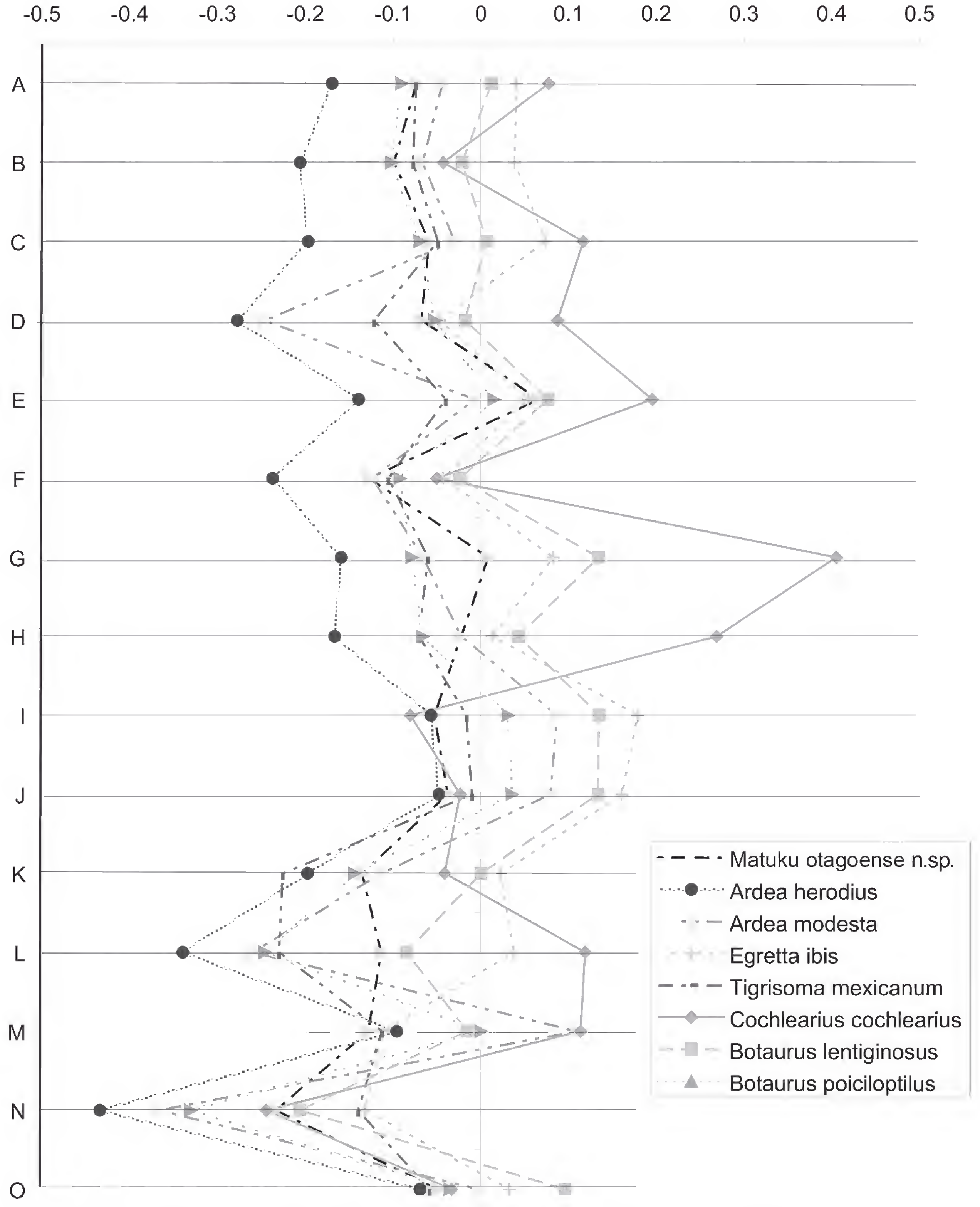

Figure 4. Ratio diagram (after Simpson, 1941) using measurements of *Nycticorax caledonicus* as the origin (i.e. log of measurement of *Nycticorax caledonicus* is equivalent to 0). This diagram indicates that the relative proportions of the fossil heron bones vary in a similar way to those of other herons and so it is likely that the fossil bones come from a single species. Abbreviations: (*A*), tarsometatarsus, maximum distal width; (*B*), tarsometatarsus, maximum distal depth; (*C*), tarsometatarsus, width of trochlea metatarsi III; (*D*), Tarsometatarsus, estimated total length; (*E*), coracoid, maximum cranial width (from hum. facet to brachial tub.); (*F*), coracoid, maximum shaft width (below procoracoid); (*G*), coracoid, length of humeral facet; (*H*), coracoid, depth of humeral facet; (*I*), quadrate, mean of 2 individuals, depth from capit. squam. to cond. lateralis; (*J*), quadrate, mean of 2 individuals, depth from capit. squam. to cond. medialis; (*K*), axis, width of facies articularis cranialis; (*L*), axis, inter-condyle distance; (*M*), axis, width of single zygapophyses caudalis; (*N*), axis, depth single zygapophyses caudalis; (*O*), axis, greatest width (across facies artic. caudalis).

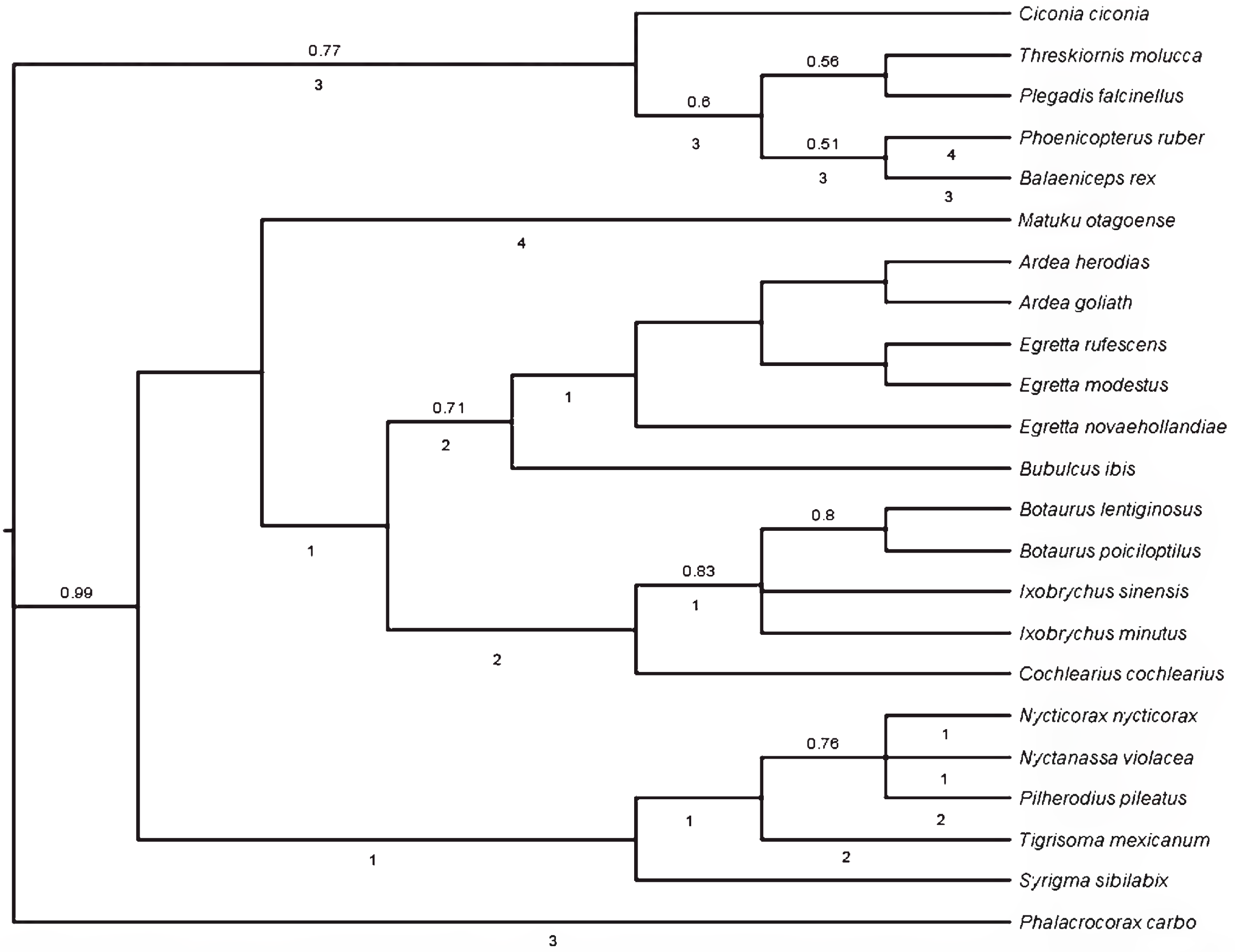

Figure 5. A strict consensus tree of the 12 shortest trees (length = 153, CI = 0.4444, HI = 0.5556, RI = 0.7222) in which the topology was constrained with Ardeidae as sister group to an outgroup comprised of the non ardeid Ciconiiformes and the pelecaniform—*Phalacrocorax carbo.* Bootstrap support values (> 0.50) are shown above and the number of significant (> 0.50) unambiguous apomorphies are shown below the corresponding node.

Are the elements from the same species?

Comparison of available measurements from *Matuku* (Fig. 4) with those of living species of heron using Simpson Ratio diagrams (Simpson, 1941), suggests that these elements are probably from the same species as they co-vary from the standard taxon in a fashion consistent to that seen in other taxa.

Phylogenetic analyses

We defined 50 multistate characters and coded these for 18 ingroup and six outgroup taxa. The non-ardeid Ciconiiformes, the pelecaniform and the phoenicopteriform were defined as the outgroup. The remaining 18 terminal taxa, including the four extant Recent New Zealand herons and the fossil taxon, were unconstrained.

We tried including *Scopus* in the data set and found that it tended to have a sister relationship to herons in preliminary analyses, but in the present dataset its inclusion introduced conflict in the data causing a polytomy of it and the main heron clades. For this reason we present the analyses with it excluded. Similarly, preliminary analyses with all characters unordered resulted in 562 shortest trees, length 146. But when 19 characters (characters 1, 2, 4, 6–14, 18, 19, 23, 25, 35, 36, 47) that clearly formed morphoclines, were treated as ordered, the analysis retrieved just 12 shortest trees, length 153, for which a strict consensus tree was completely resolved. For this our preferred tree, we show bootstrap support (1000 bootstrap replicates of the Heuristic search) and the numbers of unambiguous apomorphies supporting each node (Fig. 5).

Our strict consensus tree of the 12 shortest trees retrieved three major clades of herons with significant bootstrap support: 1 a bittern clade (bootstrap 83%), egrets and day herons (bootstrap 71%), and a clade of night herons (bootstrap 76%) (Fig. 5). Although we used few elements and, in general, only scored characters that were present in our poorly preserved fossil specimens, our analysis does not support the monophyly of the true day herons (Tribe Ardeini; Kushlan & Hancock, 2005), despite this group being only represented by *Ardea* in our analyses, but does support the monophyly of the bittern subfamily Botaurinae. Like many other authors, we find the genera *Ardea* and *Egretta* to both be polyphyletic. The boat-billed heron was found to be sister to the bittern clade, but this relationship was weak (bootstrap < 50%; 4 unambiguous apomorphies).

Matuku otagoense is strongly supported as a member of the Ardeidae (Bootstrap 99%), but there is no support for it being a member of the *Ardea-Egretta* clade (Bootstrap = 71%, 2 unambiguous apomorphies), the bittern clade (Bootstrap = 83%, 3 unambiguous apomorphies), or the night herons *Nycticorax, Nyctinassa* and *Pilherodius* (Bootstrap = 76%, 3 unambiguous apomorphies). However, 4 unambiguous apomorphies support *Tigrosoma* joining the

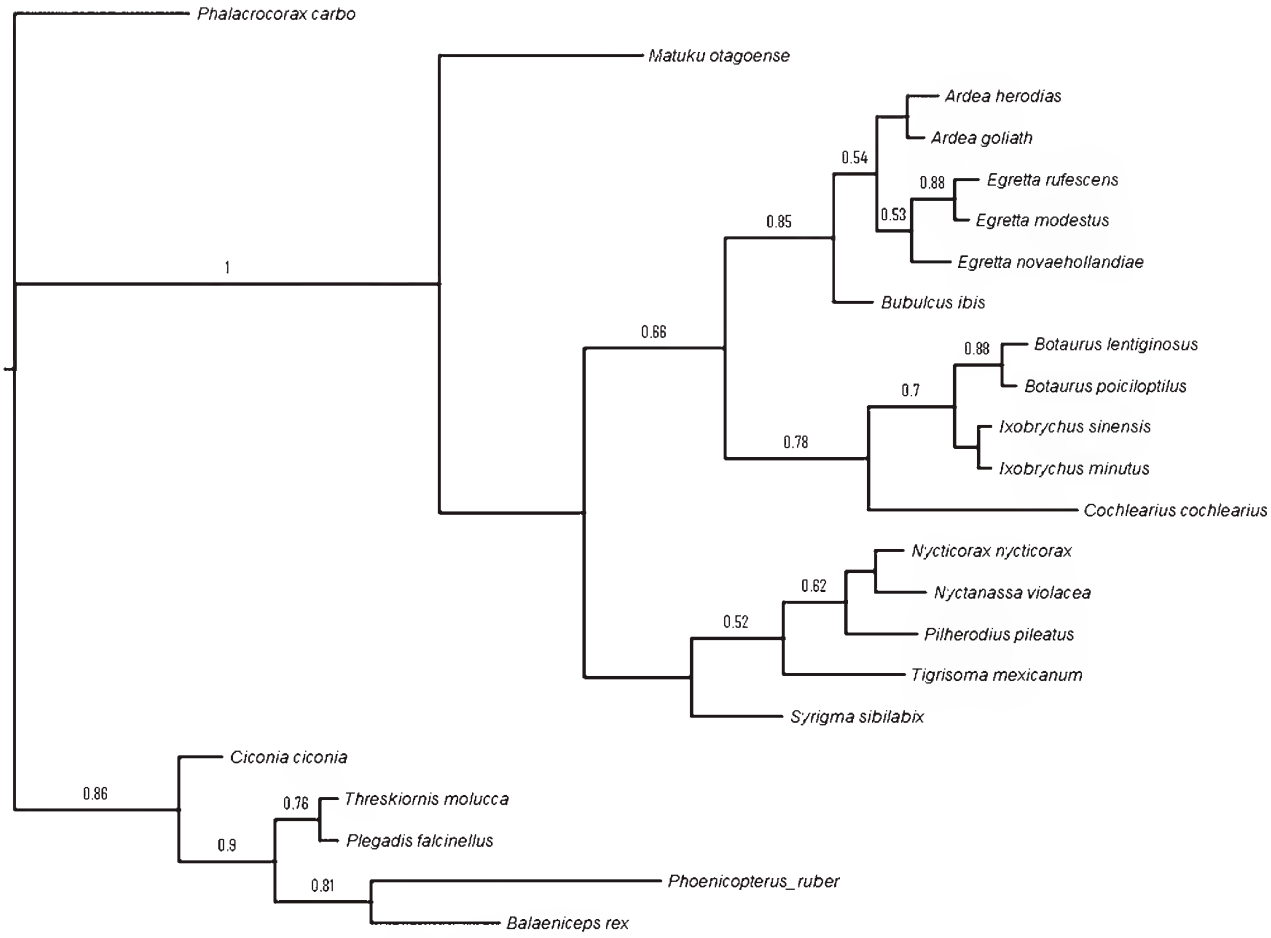

Figure 6. A Bayesian consensus tree derived from 4,001 trees sampled: Run 1 (mean = –546.302, s.d. = 0.099, Effective Sample Size = 3208.424); Run 2 (–546.223, 0.113, 2388.97). Support values are shown above the corresponding node.

night herons as a clade, and 2 unambiguous apomorphies support *Syrigma* joining this enlarged night heron clade to the exclusion of the St Bathan's heron. There is no support (no unambiguous apomorphies, Bootstrap < 50%) for *Matuku otagoense* forming a clade with egrets and bitterns sister to night herons. and there is only limited support for a clade of egrets and bitterns to the exclusion of SB heron (1 unambiguous apomorphy, Bootstrap = 0.250).

A Bayesian consensus tree derived from 4,001 trees sampled after the burnin period has credibility values (percentage posterior probabilities) exceeding 0.50 as shown in Fig. 6. The probability plot in Tracer plateaued by 250,000 generations, so the burnin discard of 1,000,000 generations was more than adequate. The two runs achieved stationarity and convergence: log likelihood statistics (LnL) after Burnin = 4001 for Run 1 (mean = –546.302, s.d. = 0.099, Effective Sample Size = 3208.424); Run 2 (–546.223, 0.113, 2388.97), and after 5,000,000 generations the average standard deviation of split frequencies was 0.03750, well within the recommended cutoff value of < 0.1.

The Bayesian consensus tree (Fig. 6), retrieved the same three well supported clades as the parsimony analysis and differed in topology from the parsimony consensus tree (Fig. 5) only in the branching order of the three main clades and in which nodes all had weak Bootstrap support. This is unlikely to be the result of missing data in *Matuku* as only four characters are missing thus we consider that this data set simply is not adequate to resolve these deeper relationships.

So in summary these analyses show that *Matuku otagoense* is a member of Ardeidae but is there is no support for a sister group relationship with any of the main groups of herons.

Discussion

The finding of a heron in the St Bathans Fauna is not surprising given the lacustrine nature of the sediments, but highlights once again the significance of this, New Zealand's only tertiary terrestrial fossil assemblage (Worthy *et al.*, 2007). It is noteworthy however that these layers have revealed thousands of avian fossils, but the seven isolated bones of *Matuku otagoense* described here are the only heron remains identified to date.

This is the first fossil ardeid that we are aware of whose relationships have been determined by phylogenetic analysis. The majority of previous fossil specimens have been referred to either *Ardea* or *Nycticorax*, but most were not assigned to genera or subfamily by shared apomorphies and thus we consider their relationships to be uncertain. Our analyses reveal phylogenetic relationships (Figs 5, 6) that indicate no support for the inclusion of *Matuku otagoense* within any extant genus or clade and that it was not closely related to any living taxon. We consider this more than adequate evidence for the erection of a new genus, *Matuku*.

The fossil record of ardeids older than the Early Pleistocene is sparse, although they have been recorded as far back as the Eocene and from several continents (North America, Europe—or Eurasia, Africa) (Table 1). The St Bathans fossil is the first ardeid identified in the Tertiary of Australasia and its basal placement may be significant in calibrating the molecular clock for the group.

Our Bayesian analysis found limited support for the novel result that the neotropical boat-bill heron *Cochlearius* may be sister to the Botaurinae. *Cochlearius* has generally been placed in a monotypic family, the Cochleariidae (Peters, 1931; Wetmore, 1951) until E. Mayr & Amadon (1951) reduced it to subfamily level in the Ardeidae. Bock (1956) then went further and included it within Nycticoracinae. Payne & Risley (1976) and Payne (1979) placed it in a tribe, Cochlearini, related to but separate from night-herons, based on a combination of morphological and plumage characters. Some osteological (Cracraft, 1967; Livezey & Zusi, 2007) and genetic work (Sheldon *et al.*, 2000) has shown that it may be separate from Nycticoracinae and perhaps has a closer relationship to Tigrisominae (Sheldon, 1987; Sheldon *et al.*, 1995; McCracken & Sheldon, 1998). Until now no one has suggested as far as we are aware any relationship between boat-bill herons and the bitterns.

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Appendix 1

List of characters used in phylogenetic analysis.

1 **Tarsometatarsus, distal end, plantar aspect**. Sulcus on trochlea metatarsi IV:
   - 0 Absent
   - 1 Weak
   - 2 Strong

2 **Tarsometatarsus, distal end, plantar aspect**. Sulcus on trochlea metatarsi III:
   - 0 Absent
   - 1 Weak
   - 2 Strong

3 **Tarsometatarsus, distal end, dorsal aspect**. Position of distal foramen (foramen vasculare distale) relative to the proximal end of trochlea metatarsi III:
   - 0 Equal
   - 1 More proximal, with distal margin of foramen level with proximal margin of trochlea
   - 2 More distal

4 **Tarsometatarsus, distal end, dorsal aspect**. Size and shape of distal foramen:
   - 0 Absent
   - 1 Small and circular
   - 2 Large and slit shaped

5 **Tarsometatarsus, distal end, dorsal aspect**. Distal foramen, branching canal opening into inter-trochlear incision from main dorso-plantar canal:
   - 0 Closed dorsally
   - 1 Open dorsally, thus forming a notch

6 **Tarsometatarsus, distal end, dorsal aspect**. Orientation of trochlea metatarsi III relative to the axis of the shaft (corpus tarsometatarsi):
   - 0 Parallel
   - 1 Slightly bent laterally
   - 2 Strongly bent laterally

7 **Tarsometatarsus, distal end, dorsal aspect**. Protrusion of trochlea metatarsi II from the medial margin of the shaft (corpus tarsometatarsi):
   - 0 Does not protrude
   - 1 Gradually protrudes
   - 2 Abruptly protrudes

     profile of trochlea on medial side meets shaft at distinct angle

8 **Tarsometatarsus, distal end, dorsal aspect**. Protrusion of trochlea metatarsi IV from the lateral margin of the shaft (corpus tarsometatarsi):
   - 0 Does not protrude
   - 1 Protrudes gradually
   - 2 Protrudes abruptly

9 **Tarsometatarsus, distal end, plantar aspect**. Fossa metatarsal I:
   - 0 Absent
   - 1 Shallow
   - 2 Deep

10 **Tarsometatarsus, shaft, dorsal aspect**. Dorso-plantar compression of the proximal medial side of the shaft adjacent to the tuberositas m. tibialis cranialis:

- 0 None, shaft thick
- 1 Weak, i.e. Botaurus
- 2 Strong such that the medial margin is essentially a crest

  Note, this is related to the depth of the fossa parahypotarsalis medialis

11 **Tarsometatarsus, shaft, dorsal aspect**. Dorsal metatarsal groove (sulcus extensorius):

- 0 Absent
- 1 shallow
- 2 Deep

12 **Tarsometatarsus, shaft, plantar aspect**. Plantar metatarsal groove (sulcus flexorius):

- 0 Absent
- 1 Shallow
- 2 Deep

13 **Tarsometatarsus, shaft, plantar aspect**. Crista plantaris lateralis:

- 0 Absent
- 1 Weakly developed
- 2 Strongly developed

14 **Tarsometatarsus, proximal end, plantar aspect**. Hypotarsus, length relative to width [Character 2269 of Livezey & Zusi (2007)]:

- 0 Length greater than width
- 1 Length slightly less than width
- 2 Length significantly less than width

15 **Tarsometatarsus, proximal end, proximal aspect**. Hypotarsus entirely plantar of corpus, and depth [Character 2270 of Livezey & Zusi (2007)]:

- 0 Distinctly less than that of corpus
- 1 Approximating corpus
- 2 Greater than that of corpus

16 **Tarsometatarsus, proximal end, plantar aspect**. Hypotarsus, sulcus for shallow flexor tendons fpp2/fp2 (flexor perforans et perforatus digiti II, flexor perforatus digiti II). [This is the tendinal passage 2 of Strauch (1978: fig. 29C). *Tigrisoma* has a single sulcus plantar of tc1 but which sulcus is slightly divided by a low ridge on the medial calcaneal ridge indicating 2 tendons in this sulcus, presumably 2 and 6 Character modified from character 2279 of Livezey & Zusi (2007)]:

- 0 Absent
- 1 Distinct sulcus separated from sulcus for more lateral fp3/fp4 (flexor perforatus digiti III et IV)
- 2 Enclosed or near enclosed canal

17 **Coracoid, extremitas omalis, medial aspect**. Sulcus musculi supracoracoideus:

- 0 No foramen below clavicular facet (facies articularis clavicularis)
- 1 Foramen immediately below dorsal margin of the clavicular facet
- 2 Foramen immediately below ventral margin of the clavicular facet

18 **Coracoid, extremitas omalis, medial aspect**. Proc. acrocoracoideus, and supracoracoidal sulcus—lateromedial compression across the transverse plain:

- 0 Absent
- 1 Weakly or not compressed thus essentially circular
- 2 Moderately compressed

19 **Coracoid, extremitas omalis, dorsal aspect**. Acrocoracoid—impressio ligamenti acrocoracohumeralis:

- 0 Absent
- 1 Shallow
- 2 Deep

20 **Coracoid, extremitas omalis, dorsal aspect**. Distance from omal end of facies artic. humeralis to tip of proc. acrocoracoideus:

- 0 Equal to dorsoventral depth of clavicle facet (facies artic. clavicularis)
- 1 Less than half of depth of clavicle facet

21 **Coracoid, extremitas omalis, procoracoidal process**. Ventrally, a concave groove forming a caudal extension of supracoracoidal sulcus. [Character 1285 (in part) of Livezey & Zusi (2007)]:

- 0 Absent
- 1 Present

22 **Coracoid, extremitas omalis, procoracoidal process**. Extends cranomedially of the scapular cotyla forming a flattened tuberculum apicalis procoracoidei. [Character 1289 of Livezey & Zusi (2007)]:

- 0 Absent
- 1 Present

23 **Coracoid, extremitas omalis, medial aspect**. Sulcus musculi supracoracoideus:

- 0 Smooth
- 1 Slight ridge running sternally, barely dividing sulcus into dorsal and ventral segments
- 2 Strong ridge bisecting sulcus

24 **Coracoid, shaft, dorsal aspect**. Foramen nervi supracoracoidei:

- 0 Absent
- 1 Present

25 **Coracoid, shaft, dorsal aspect**. Extent of procoracoid sternally along shaft:

- 0 No extension, very short
- 1 Elongate, extends for less than half the length of shaft
- 2 Elongate, extends for greater than half length of shaft

26 **Os quadratum, rostral aspect**. Caput squamosum:

- 0 Rounded
- 1 Triangular, broader at top, draws to point laterally/ventrally

27 **Os quadratum, lateral aspect**. Tubercle at dorsal end of crista tympanica:

- 0 Absent
- 1 Immediately ventral of caput squamosum
- 2 Present, separated from caput squamosum

28 **Os quadratum, medial aspect**. Foramen pneumaticum mediale:

- 0 Situated between crista tympanica and crista medialis
- 1 Situated rostrally of crista medialis

29 **Os quadratum, medial aspect**. Foramen pneumaticum mediale when situated at intersection of crista tympanica and crista medialis:

- 0 Very small
- 1 Large
- 2 Not so placed

30 **Os quadratum, medial aspect**. Tubercle at dorsal end of crista medialis immediately ventral of caput oticum:

- 0 Absent
- 1 Present

31 **Os quadratum, ventral aspect**. Tubercle on depressio praecondylaris immediately caudad to medial condyle:

- 0 Absent
- 1 Present

32 **Os quadratum, ventral aspect**. Vallecula intercondylaris:

- 0 Area simply a shallow sulcus
- 1 Forms fossa bounded on rostral edge by raised crista
- 2 Shallow fossa with narrow sulcus onto rostral surface
- 3 Deep and U shaped fossa, opening with wide sulcus onto rostral surface

33 **Os quadratum, caudal aspect**. Prominent sulcus between condylus lateralis and condylus caudalis running up to edge of crista lateralis:

- 0 Absent
- 1 Present

34 **Axis, cranial aspect**. Dens:

- 0 Wider than facies articularis atlantica
- 1 Not so

35 **Axis, ventral aspect**. Ratio of width of facies artic. cranialis to distance from facies artic. cranialis to caudalmost edge of facies artic. caudalis:

- 0 Greater than or equal to 35% (i.e. centrum fat and wide)
- 1 Less than 35% but greater than 25% (i.e. relatively long and narrow)
- 2 Less than 25% (i.e. very long and narrow)

36 **Axis, ventral aspect**. Zygapophyses caudalis (postzygapophysis) shape: ratio of width to length:

  0 Circular (ratio greater than 100%)
  1 Oval (ratio greater than 70% but less than 100%)
  2 Teardrop or elongate (ratio less than 70%)

37 **Axis, dorsal aspect**. Zygapophyses cranialis (prezygapophysis) shape (ratio of width to length):

  0 Tending circular (ratio greater than 70%)
  1 Elongate (ratio less than 70%)

38 **Axis, dorsal aspect**. Proximal (or cranial edge) of arcus atlantis (neural arch):

  0 Concave
  1 Straight

39 **Axis, dorsal aspect**. Zygapophyses caudalis prominent laterally relative to facies at mid length:

  0 Not so
  1 Yes

40 **Axis, ventral (or dorsal) aspect**. Zygapophyses cranialis extend laterally of lateral profile as distinct processes:

  0 No
  1 Yes

41 **Axis, lateral aspect**. Processus spinosus (anapophysis), dorsal profile between zygapophyses:

  0 With distinct convex profile (markedly raised anteriorly, not flat)
  1 Lacking convex profile

42 **Axis, lateral aspect**. Processus spinosus (anapophysis):

  0 Starts immediately posteriad of zygapophyses cranialis
  1 Starts farther posteriad, so initially flat

43 **Axis, lateral aspect**. Facies artic. cranialis:

  0 Roughly at right angles to axis of bone
  1 Sloped anteroventrally

44 **Axis, lateral and dorsal aspects**. Dens:

  0 Greater than length of zygapophyses cranialis
  1 Less than length of zygapophyses cranialis

45 **Axis, lateral aspect**. Corpus ventralis, foramen transversarium:

  0 Complete, enclosed laterally
  1 Incomplete, open laterally, forming sulci

46 **Axis, lateral aspect**. Corpus ventralis, pneumatic fossa:

  0 Absent
  1 Present laterally, secondary sulci are present posteriorly

47 **Rostrum mandibulae, dorsal aspect**. Pars symphysialis, length of zone of fusion:

  0 Considerably greater than transverse width
  1 Approximately equal to transverse width
  2 Transverse width considerably greater

48 **Rostrum mandibulae, dorsal aspect**. Shape:

  0 Narrow and thin
  1 Broad and bulbous
  2 Wide and deep, extremely modified

49 **Rostrum mandibulae, lateral aspect**. Os dentale:

  0 Foramina densely cover whole lateral surface
  1 Prominent foramina mainly along cutting edge
  2 Foramina indistinct

50 **Rostrum mandibulae, dorsal aspect**. Pars symphysialis, relative width of symphysis:

  0 Narrow (ratio of width to length < 5)
  1 Broad (ratio of width to length > 5)

Appendix 2

Character matrix of 50 morphological characters used for phylogenetic analyses. Symbols used in matrix: * = (01); + = (12).

	1	1111111112	2222222223	3333333334	4444444445
	1234567890	1234567890	1234567890	1234567890	1234567890
Matuku otagoense n.sp.	220100101?	102???0101	1000001001	1301111110	0100000011
Ardea herodias	1102111112	1020110110	1000010000	1201221110	1111010010
Ardea goliath	1101111212	1020110110	1000010000	1201221110	1111010010
Egretta rufescens	1121111211	1020110210	1000010000	0201221110	1111110010
Ardea modestus	1121111211	10201102*0	1000010000	0201221110	1111010010
Egretta novaehollandiae	110111121*	1020110110	1000010000	0201121110	1011010010
Ardea ibis	1101111012	1020110110	1000010000	0201111110	1111010010
Nycticorax nycticorax	2211102012	*01011021*	0000001010	12010+1010	011001001*
Nyctanassa violacea	2211102012	0010110111	0000001010	1201010010	0111010011
Pilherodius pileatus	2201102022	0011110211	0000001010	1201021010	0111110011
Tigrisoma mexicanum	2221102112	1010210210	1100011010	1201121010	0011010011
Botaurus lentiginosus	2221020011	1021220110	0100010000	1201221110	1111110011
Botaurus poiciloptilus	2221020011	1021220120	0100010000	1201221110	1111110011
Ixobrychus sinensis	2221121011	1021220120	0100010000	1201221110	1111010011
Ixobrychus minutus	2221121011	1021220120	0100010000	1201221110	1111010011
Cochlearius cochlearius	2101120011	2021210020	0100001021	0201011110	1111010111
Syrigma sibilabix	2221022010	1010110211	1000000000	0201021010	0111010011
Scopus umbretta	2211101011	1020201010	1000000000	1201020110	1111102111
Ciconia ciconia	2212001101	2110100220	*110101121	0000021001	1111100011
Threskiornis molucca	1111002111	2120102220	1111101121	0000021001	1111100011
Plegadis falcinellus	1111002111	2120102120	1111101121	0000021001	1111100011
Phoenicopterus ruber	1122102201	0120100020	1121101121	0010001000	1111102201
Phalacrocorax carbo	2212010110	2020100200	0000001121	0110001001	1111100010
Balaeniceps rex	1111010110	1020100120	1111101121	10000200*1	1111102111

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Moa's Ark: Miocene Fossils Reveal the Great Antiquity of Moa (Aves: Dinornithiformes) in Zealandia

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ABSTRACT. Fossil eggshell and bone fragments from New Zealand's Miocene St Bathans Fauna indicate that two taxa of giant flightless moa (one weighing 20–25 kg and another much larger than this) were present in Zealandia 19–16 Ma. Contrary to recent suggestions, we conclude that moa have a long history in Zealandia, almost certainly extending to before the Oligocene "drowning". This conclusion is consistent with biotic evidence from other sources, which indicates a great antiquity of several Zealandian animals and plants.

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Moa (Dinornithiformes) have been central to the debate around the antiquity of the terrestrial New Zealand biota—so much so that their presumed Gondwanan origins have seen the country sometimes dubbed "Moa's Ark" (Brewster, 1987; Bellamy *et al.*, 1990). Although numerous taxa have generally been considered to have dispersed over-water to Zealandia, the biota has long been assumed to include Gondwanan vicariant ancestors of some plants (e.g., southern beech *Nothofagus*), many invertebrates (e.g., velvet worms *Peripatus* and hyriid freshwater mussels), New Zealand frogs (leiopelmatids), tuatara (sphenodontids) and moa (e.g., Fleming, 1979).

The order Dinornithiformes (superorder Palaeognathae) includes nine Recent species of moa, all of which became extinct about 600 years ago as a result of human hunting (Tennyson & Martinson, 2007; Bunce *et al.*, 2009). Their remains are numerous in Late Pleistocene-Holocene fossil deposits (Worthy & Holdaway, 2002; Tennyson & Martinson, 2007). Moa were very large flightless birds, varying in weight from 9–242 kg (Worthy & Holdaway, 2002; Tennyson

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& Martinson, 2007). Worthy *et al.* (1991) summarized knowledge of Pliocene-Pleistocene moa fossils (then the oldest moa known) but these were morphologically similar to Recent taxa and not particularly informative with respect to the origins of moa. No older moa material was described until our research of the late Early Miocene St Bathans Fauna began in 2001, the first remains recovered being eggshell only (Worthy *et al.*, 2002, 2007; Pole *et al.*, 2003).

The history of New Zealand as a separate landmass began when the continental fragment called Zealandia split away from the Australis section of East Gondwana (see Gibbs, 2006). This rifting occurred between the Late Cretaceous and Early Eocene 83–52 Ma (Gaina *et al.*, 1998). According to the current paradigm, the continent of Zealandia slowly sunk and land area reached its minimum extent in the Oligocene, when it was reduced to perhaps 18% of its current area, before rising again to its present level (Cooper & Cooper, 1995).

Pole (1994) reignited a longstanding debate about the origins of New Zealand's flora and fauna by postulating that the entire forest flora, and perhaps the whole terrestrial biota, arrived by long-distance dispersal. This theory has been built on by others (e.g., Campbell & Landis, 2001; Waters & Craw, 2006; Campbell & Hutching, 2007; Trewick *et al.*, 2007; Campbell *et al.*, 2008) and comprehensively presented by Landis *et al.* (2008), who suggested that the marine drowning of Zealandia at the Oligocene-Miocene boundary (25–22 Ma) was complete, based primarily on geological evidence of Tertiary wave cut platforms and extensive Oligocene marine limestone deposits (and a concurrent absence of terrestrial deposits). In addition, some genetic studies have indicated the relatively recent arrival of the ancestors of supposedly Gondwanan modern-day taxa and post-Oligocene radiations, notably for one classic example: *Nothofagus* beech (e.g., Cooper & Cooper, 1995; Cook & Crisp, 2005; Knapp *et al.*, 2005; Goldberg *et al.*, 2008; but see Heads, 2006). An increasingly popular assertion is that there is no vicariant Gondwanan biota represented by descendants in the Recent New Zealand biota and that all terrestrial taxa, including the ancestors of moa, arrived via dispersal.

A long-standing but controversial theory is that the Recent palaeognaths (tinamou Tinamidae, moa, kiwi Apterygidae, cassowary and emu Casuariidae, ostrich Struthionidae, rhea Rheidae, elephant bird Aepyornithidae) attained their present distributions through vicariance as the southern super-continent Gondwana broke apart (e.g., Cracraft, 2001; Grellet-Tinner, 2006). Although details of these events and the relationships between palaeognaths are hotly debated (e.g., Harshman *et al.*, 2008; Phillips *et al.*, 2010), there is much continued support for a Cretaceous origin of palaeognaths (e.g., Cooper & Penny, 1997; Phillips *et al.*, 2010) and the great antiquity of moa in Zealandia (e.g., Haddrath & Baker, 2001).

If the ancestors of moa arrived in Zealandia after the Oligocene, they presumably arrived by flying (Pole, 1994; Waters & Craw, 2006), since during the Oligocene and ever since, emergent Zealandia has been 1,850 km from the nearest Australian land (Stevens, 1980). Some proponents of the post-Oligocene arrival theory have stated recently that the oldest known moa fossils are only 1.5 Ma (Landis *et al.*, 2008), with Goldberg *et al.* (2008) declaring that "there is as yet no direct evidence… that their pre-Pleistocene ancestors were giants", contrary to information in Worthy *et al.* (2007) and preceding abstracts in the geological literature (e.g., Jones *et al.*, 2002; Worthy *et al.*, 2002). Campbell & Landis (2008) concluded that "The giant extinct flightless bird, the moa, may be an evolutionary phenomenon of the past 23 million years".

Here, we challenge these assertions by presenting evidence of the presence of large, flightless moa in Zealandia during the late Early Miocene.

New Zealand has an extensive Late Pleistocene-Holocene terrestrial vertebrate fossil record younger than 25,000 years but, until recently, the Tertiary (65–2.6 Ma) avifauna record was restricted to marine birds (Worthy & Holdaway, 2002). However, the late Early Miocene (19–16 Ma) St Bathans Fauna of Central Otago, South Island, has now revealed a diverse vertebrate fauna dating from just after the Late Oligocene "drowning" event (Worthy *et al.*, 2006, 2007, 2008, 2009; Jones *et al.*, 2009). Thousands of bird bones have been recovered from at least 30 taxa, as well as hundreds of pieces of bird eggshell.

Methods

The St Bathans Fauna has been recovered from three main fossil sites near St Bathans: 1, Manuherikia River = various "HH" sites; 2, Mata Creek, which includes the "Croc Site"; 3, Vinegar Hill (for detailed information on localities see Worthy *et al.*, 2007). The terrestrial vertebrate remains are found mainly in sandy layers and were deposited in a large paleo-lake. Owing to reworking and transport resulting from water movement at the lake edge, there is no articulation of specimens and all fossils are less than 15 cm long. Our excavations were carried out between the years 2001–2009, using an excavator to remove alluvial over-burden, followed by hand-excavation of thin sandy layers, wet sieving of sediment using 1–4 mm mesh, drying and subsequent sorting under magnification in labs.

We studied the fossil record of moa from the St Bathans Fauna to determine how it contributes to the debate on the "drowning" of Zealandia, specifically looking at the size of these moa and how this information contributes to our understanding of the time of their arrival in Zealandia. We re-examined purported moa eggshell from the deposits (Worthy *et al.*, 2007) and also studied newly discovered material, including some large bone fragments. All measurements were taken with vernier callipers.

The structure of eggshell collected in 2001–2007 was examined and its thickness measured. Excavations in 2008–2009 have recovered many more pieces of eggshell but these remain to be fully sorted and studied in detail. Initially we divided the eggshell into two groups based on thickness. Measurements were taken at the least damaged point on the edge of each fragment but, because of wear, some measurements may be under-estimates. We then examined the structure of some of the thicker specimens. In order to obtain fresh surfaces exposing the internal crystalline structure of the eggshell for examination by scanning electron microscopy (SEM), specimens were washed and air dried and small portions were carefully broken off with tweezers. These broken fragments were mounted securely on aluminium SEM stubs with carbon tape and carbon coated. All specimens were examined using the LEO 440 SEM at the Institute of Geological & Nuclear Sciences. Specimens from the same collection location could be from the same egg but generally it was not possible to associate fragments

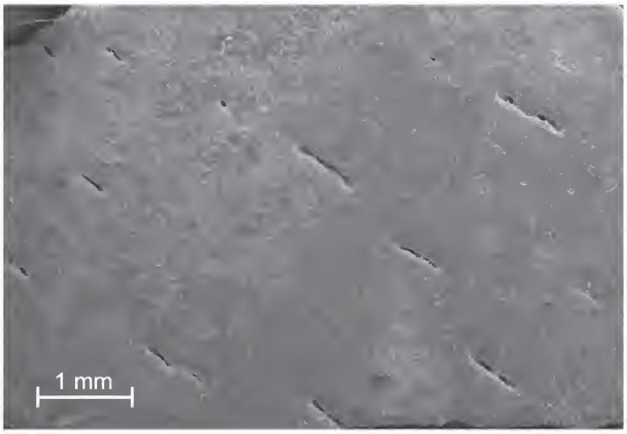

Figure 1. SEM of the external surface of "thick" Miocene fossil eggshell from the St Bathans deposits (NMNZ S.44766) showing the characteristic elongate pore-depressions, smooth surface and lack of ornamentation.

and they are treated here as independent specimens unless noted in Appendix 1.

Bone fragments large enough to be potentially from moa were compared with Pleistocene and Recent avian material in the Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand (NMNZ).

Results

We list 154 pieces of eggshell (Appendix 1) and six bone fragments (Table 3) that we consider likely to be from moa. These eggshell remains were recovered from about 10 m^3 of deposit excavated in 2001–2007, giving an average rate of occurrence of about 15 pieces per m^3.

Eggshell

Comparison of palaeognath eggshell structure. In cross-section, the Miocene St Bathans eggshell shows distinct layers that identify it as avian and rule out testudines and crocodilians (Williams & Vickers-Rich, 1991; Mikhailov, 1992, 1997; Grellet-Tinner, 2006); crocodilians are also represented in the fauna by fossil bones (Molnar & Pole, 1997; Worthy *et al.*, 2009).

The most common thin eggshell found in the St Bathans deposits has tiny circular surface pore-depressions spaced about 1 mm apart and three internal layers in cross-section, with the inner mammillae wider than high. These structures are found in most neognaths, so this fossil eggshell is presumed to be mainly from the abundant anatids found in this fauna (Jones *et al.*, 2002; Worthy *et al.*, 2007). Our analysis focuses on the rarer thicker eggshell found in the St Bathans deposits.

The "thick" fossil eggshell has a smoothly homogeneous surface structure and sometimes slit-like surface pore-depressions (see Fig. 1), as found in moa, rhea and elephant bird eggs (e.g., Hutton, 1872; Gill, 2007; also see Appendix 2). The pore-depressions can be up to 1.1 mm long and sometimes densely-spaced (e.g., 0.5 mm apart) but the pores on other fragments have more oval surface depressions and occur at a lower density.

Scanning electron microscopy of a piece of the "thick" fossil eggshell (see Fig. 2, also Worthy *et al.*, 2007, fig. 18E, which is a thin section of the same piece of eggshell) facilitates examination of its internal structure. It has three layers and thus is similar in structure to most palaeognath eggshell (Mikhailov, 1997; Zelenitsky & Modesto, 2003; Grellet-Tinner, 2006): (1) a thick innermost lower mammillary zone (MZ) with mammillae higher than wide (unlike neognaths); (2) a thick squamatic "spongy" zone (SZ) outside the MZ; and (3) a thin external zone (EZ) (see Fig. 2). Tyler (1957) and Mikhailov (1992, 1997) failed to detect the EZ layer in moa eggshell but subsequent studies have detected it (e.g., Grellet-Tinner, 2006). Contrary to our earlier finding (Jones *et al.*, 2002), the "thick" St Bathans Miocene eggshell also has an EZ.

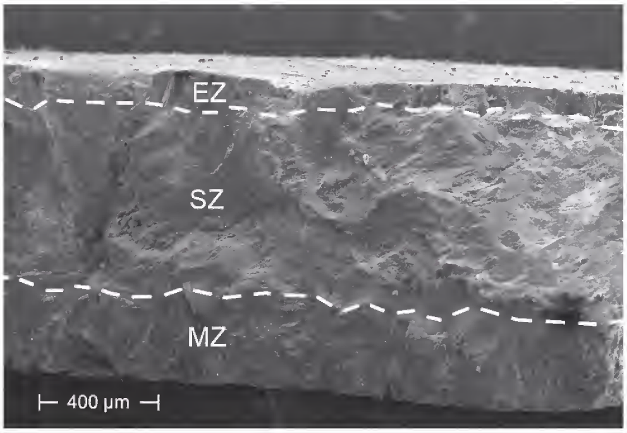

Figure 2. SEM image of a broken cross-section of "thick" Miocene fossil eggshell from the St Bathans deposits (NMNZ S.40938.9) showing the structure. The upper surface is the external layer of the shell. EZ = external zone, SZ = squamatic "spongy" zone, MZ = mammillary zone. Features consistent with moa eggshell include (*a*) the mammillae consisting of tabular wedges; (*b*) the mammillae being higher than wide; (*c*) the vesiculation in the MZ being weak or absent; (*d*) the absence of a resistant zone between the SZ and EZ; (*e*) the EZ being blocky (see Appendix 2).

The combination of structural features identified in the "thick" fossil eggshell is unique to that of moa eggshell (see Appendix 2).

Internal layers of the "thick" Miocene eggshell have the following thickness percentages: MZ 26.7, SZ 63.7, EZ 9.7 and ratios of SZ/MZ of 2.40 and EZ/SZ of 0.15 (calculated from cross-section of NMNZ S.40938.9). Moa have a SZ about twice as thick as the MZ (Hutton 1872, Tyler, 1957), although some individual pieces of moa eggshell measured by Tyler (1957) and Mikhailov (1997) had a SZ/MZ ratio of about 2.5—similar to the ratio observed in the St Bathans Miocene fossil. These authors did not detect the EZ, however, and their samples may have been eroded. The ratio of SZ/MZ in other palaeognaths examined (tinamou, kiwi, cassowary, emu, ostrich, rhea, elephant bird) can vary from about 1–3.5 (Tyler & Simkiss, 1960; Mikhailov, 1997; Grellet-Tinner, 2006 and figs in Williams, 1981; Silyn-Roberts & Sharp, 1985; Zelenitsky & Modesto, 2003; also see Appendix 2 and discussion of Grellet-Tinner's [2006] character 14). Thus the "thick" Miocene eggshell has a SZ/MZ ratio consistent with palaeognaths, including moa. Moa have an EZ/SZ ratio of about 0.14–0.19 (Grellet-Tinner, 2006 and estimated from Mikhailov, 1997, fig. 1E and Zelenitsky & Modesto, 2003, fig. 2A). The ratio of the "thick" St Bathans Miocene eggshell of 0.15 falls within this range but is lower than the EZ/SZ

Table 1. Comparative thickness of Recent palaeognath and St Bathans Miocene fossil eggshell, listed from thickest to thinnest (data from Tyler & Simkiss, 1960; Silyn-Roberts & Sharp, 1985; Zelenitsky & Modesto, 2003; Gill, 2000, 2007). SB = St Bathans.

taxon	eggshell thickness (mm)
Elephant bird	3.47–3.51
Ostrich	1.74–2.23
Moa (all species)	0.54–1.89
SB Miocene fossils ("thick")	**0.58–1.68**
Rhea	0.86–1.25
Emu	0.86–1.25
Cassowary	0.75–1.09
SB Miocene fossils (common "thin")	< 0.5 mm
Kiwi	0.34–0.50
Tinamou	0.18–0.25

ratio in emus, cassowaries, kiwi and tinamou (Grellet-Tinner, 2006; also see Appendix 2 character I).

It is worth noting that the other group of giant terrestrial birds occurring in Australasia—the extinct Australian dromornithids (order Anseriformes)—also had very thick eggshell (1.0–4.1 mm) but they are not palaeognaths, so their eggshell differs from the "thick" St Bathans eggshell in structure (Williams, 1981; Williams & Vickers-Rich, 1991; Grellet-Tinner, 2006). One key difference is that they lack the EZ layer found in all palaeognaths.

Comparison of palaeognath eggshell thickness. The common fossil eggshell at St Bathans is thin (< 0.5 mm, Table 1) and presumed to be mainly from anatids (Jones *et al*., 2002; Worthy *et al*., 2007). The rarer, thicker fossil eggshell (0.58–1.68 mm) is consistent in thickness with that laid by medium-sized to large ratites and is within the range of that of moa (Table 1). Additionally, there appear to be two classes of "thick" eggshell (see Fig. 4). The most common "thick" eggshell has an average thickness of 0.94 mm (±0.12 s.d., range 0.58–1.19 mm, n = 153) (Appendix 1). The specimens measured in this study include all those measured by Worthy *et al*. (2007), with the larger sample size here exhibiting a unimodal distribution range and a slightly lower average thickness. Some eggshell at the thinner end of this range (up to about 0.7 mm thick) could belong to species other than moa (see Gill, 2010) because the internal structure of every piece was not examined. Eggshell thickness appears to be thicker when derived from larger moa species and the most common "thick" Miocene eggshell has a thickness consistent with that from a small moa (Gill, 2007; Worthy *et al*., 2007). The thickness of the Miocene eggshell is similar to that of eggshell attributed primarily to the Holocene coastal moa (*Euryapteryx curtus*) in Northland by Gill (2000, 2010).

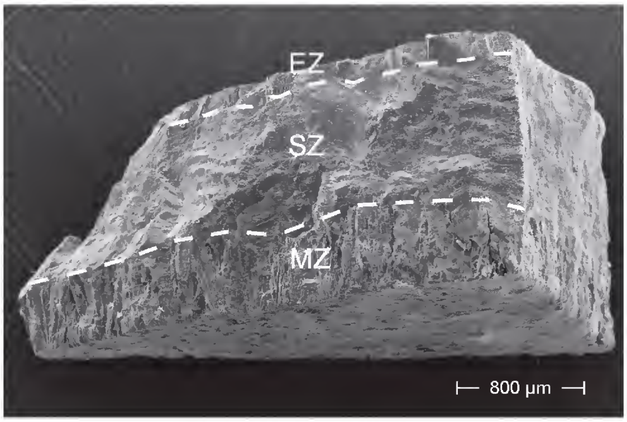

Figure 3. SEM image of a broken cross-section of the thickest piece of Miocene eggshell from the St Bathans deposits (NMNZ S.40937.2) showing the structure. The lower surface is the internal layer of the shell. EZ = external zone, SZ = squamatic "spongy" zone, MZ = mammillary zone.

Coastal moa were the smallest moa and the Northland birds weighed 12–34 kg (Worthy & Holdaway, 2002: 146–147). Therefore the most common thick Miocene eggshell in the St Bathans deposits probably represents birds in that size range, perhaps averaging about 25 kg.

A uniquely thick piece of St Bathans Miocene eggshell (NMNZ S.40937.2), at 1.68 mm, is well above the thickness range of other St Bathans fossil eggshell (see Fig. 4). Preliminary sorting of our 2008–2009 collections has not produced additional pieces of eggshell this thick. NMNZ S.40937.2 is consistent in thickness with eggshell from a bird the size of a heavy-footed (*Pachyornis elephantopus*) or giant moa (*Dinornis* spp.) (see Gill, 2007, 2010). These species are the largest moa, weighing 34–242 kg (Tennyson & Martinson, 2007). Although we earlier considered that this piece of eggshell may have been altered through diagenesis (see Worthy *et al*., 2007), there is no evidence of such alteration (see Fig. 3) and it suggests that at least two taxa, including a very large species, are represented by the "thick" eggshell from St Bathans.

Variation in frequency of occurrence of "thick" fossil eggshell between sites. The frequency of occurrence of "thick" eggshell varied considerably among the main layers at the St Bathans fossil sites (Table 2). The Manuherikia site layers HH1b ("riverbank" and "trench") and HH1d and the Vinegar Hill site were far richer in "thick" eggshell than other sites examined. Possible explanations for these differences are that "thick" eggshell may occur in sites that had either a higher energy input or a higher terrestrial (and less lacustrine) input at the time of deposition. It is notable that the HH1b

Table 2. Frequency of occurrence of "thick" Miocene eggshell in the St Bathans deposits from different layers, arranged from highest to lowest frequency.

layer	no. of "thick" eggshell specimens (A)	volume of sediment excavated 2001–2007 (B)	number of "thick" eggshell fragments per m^3 (A/B)
HH1b "riverbank"	45	ca. 0.15 m^3	300
Vinegar Hill (all sites)	31	ca. 0.2 m^3	155
HH1b "trench"	36	0.3 m^3	120
HH1d	4	ca. 0.1 m^3	40
HH1a	32	7.16 m^3	4.5
Croc site, layer 1	3	1.96 m^3	1.5

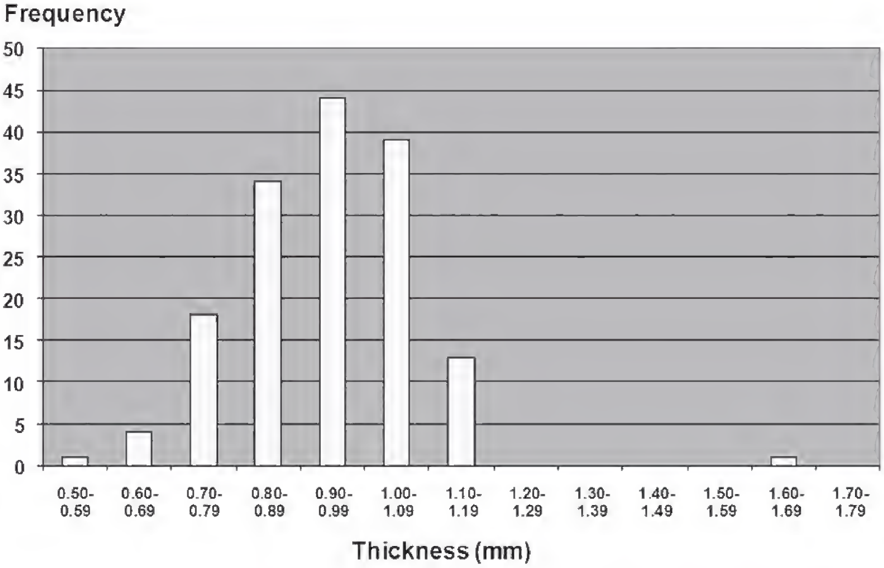

Figure 4. Distribution of thickness in a sample of 154 eggshell fragments from the Miocene St Bathans deposits (based on data in Appendix 1).

sites contain a relatively high number of quartz pebbles and heavily eroded bone, which may indicate a higher energy depositional environment. It is also notable that at least one significant terrestrial specimen has been found at Vinegar Hill (Jones *et al.*, 2009) despite the comparatively low volume of sediment excavated at this site (Table 2). Further analysis is required to understand these possible preservational trends.

Large bone fragments. Several bone fragments from the St Bathans deposits represent birds the size of moa. New Zealand's other Recent giant flightless land birds that could have had giant Miocene ancestors (adzebills *Aptornis* and geese *Cnemiornis*) have limb bones that, in parts, have a cortex thickness sometimes 5 mm or greater, so only the very thickest examples (> 4 mm) of limb bone fragments from the St Bathans deposits are noted in this study. As was found for the distribution of "thick" eggshell, the varied localities for the large bone fragments show that these remains are found at all three of the main St Bathans sites but at higher densities in the Manuherikia site layers HH1b ("riverbank" and "trench") and the Vinegar Hill site (compare Tables 2 and 3).

The most useful fragment for identifying the probable presence of large cursorial birds that might be ratites is NMNZ S.44691, which matches part of the proximal shaft of a right tibiotarsus. The shape and thickness matches the right tibiotarsus of a small moa (see Fig. 5). The position of the fibular crest relative to the ridge from the outer cnemial crest is similar to that in several palaeognaths, including tinamou, kiwi, cassowary, emu and elephant bird, but very different from that in ostrich and rhea. The size of the fragment indicates a bird of similar size to NMNZ S.447.1, which is a relatively small Holocene specimen of the moa *Megalapteryx didinus*. This species varies in weight from 14–63 kg (Tennyson & Martinson, 2007). Body mass can be calculated based on NMNZ S.447.1 having a minimum tibiotarsus shaft circumference of 67 mm. An algorithm (where mass in grams = $a.x^b$ and a = 0.076, x = minimum tibiotarsus circumference, and b = $^{2.424}$; Campbell & Marcus, 1992, table 2) gives a mass of 20.3 kg.

Apart from moa, the only other known New Zealand land birds that approach this size are extinct flightless adzebills and giant geese (Tennyson & Martinson, 2007). Both have the fibula and outer cnemial crests further apart than in the Miocene fossil and the geese have two ridges emanating from the outer cnemial crest. Probable ancestors of the giant geese have been described from the St Bathans Fauna previously (Worthy *et al.*, 2008). As these were considered to be volant, it is highly unlikely that they had a tibiotarsus as large as one represented by NMNZ S.44691.

Discussion

Before work began on the Miocene St Bathans Fauna, the oldest known moa fossils were 1.8–2.5 million years old (Worthy *et al.*, 1991; Worthy & Holdaway, 2002: 8–10). This is slightly older than the 1.5 million years noted by some Oligocene "drowning" proponents (Landis *et al.*, 2008). However, fossils indicate that the moa genera *Anomalopteryx* and *Euryapteryx* separated more than 2.5 million years ago (Worthy *et al.*, 1991) and the fossils in the St Bathans deposits now strongly suggest that moa were present in Zealandia at least 19–16 Ma. Additionally, it is worth noting that a fossil toe bone of Late Cretaceous age (80–65 Ma) from Hawkes Bay, New Zealand, may be from a very large bird (Scarlett & Molnar, 1984).

The most common "thick" eggshell (which has a structure consistent only with moa) and the large tibia fragment from the St Bathans deposits suggest that in the late Early Miocene some moa weighed about 20–25 kg, not as large as the largest

Table 3. Likely moa bone fragments from the Miocene St Bathans deposits (long bone shaft fragments are listed if their cortex thickness is > 4 mm).

NMNZ S.	site	description
40968.1	HH1b "riverbank"	long bone shaft (maximum cortical thickness 4.3 mm)
42812	Croc Site, layer 1	?distal right tibiotarsus shaft (maximum cortical thickness 4.4 mm); preserves what appears to be a fossa for an unfused ascending process of the astragalus, so represents an immature bird
44691	Vinegar Hill, site 2	proximal right tibiotarsus shaft (maximum cortical thickness 7.9 mm)
50271	HH1a	long bone shaft (maximum cortical thickness 4.7 mm)
51323	HH1b "trench"	skull element; ?left nasal; 35 x 12 mm; its poor state of preservation does not allow us to identify this element with certainty

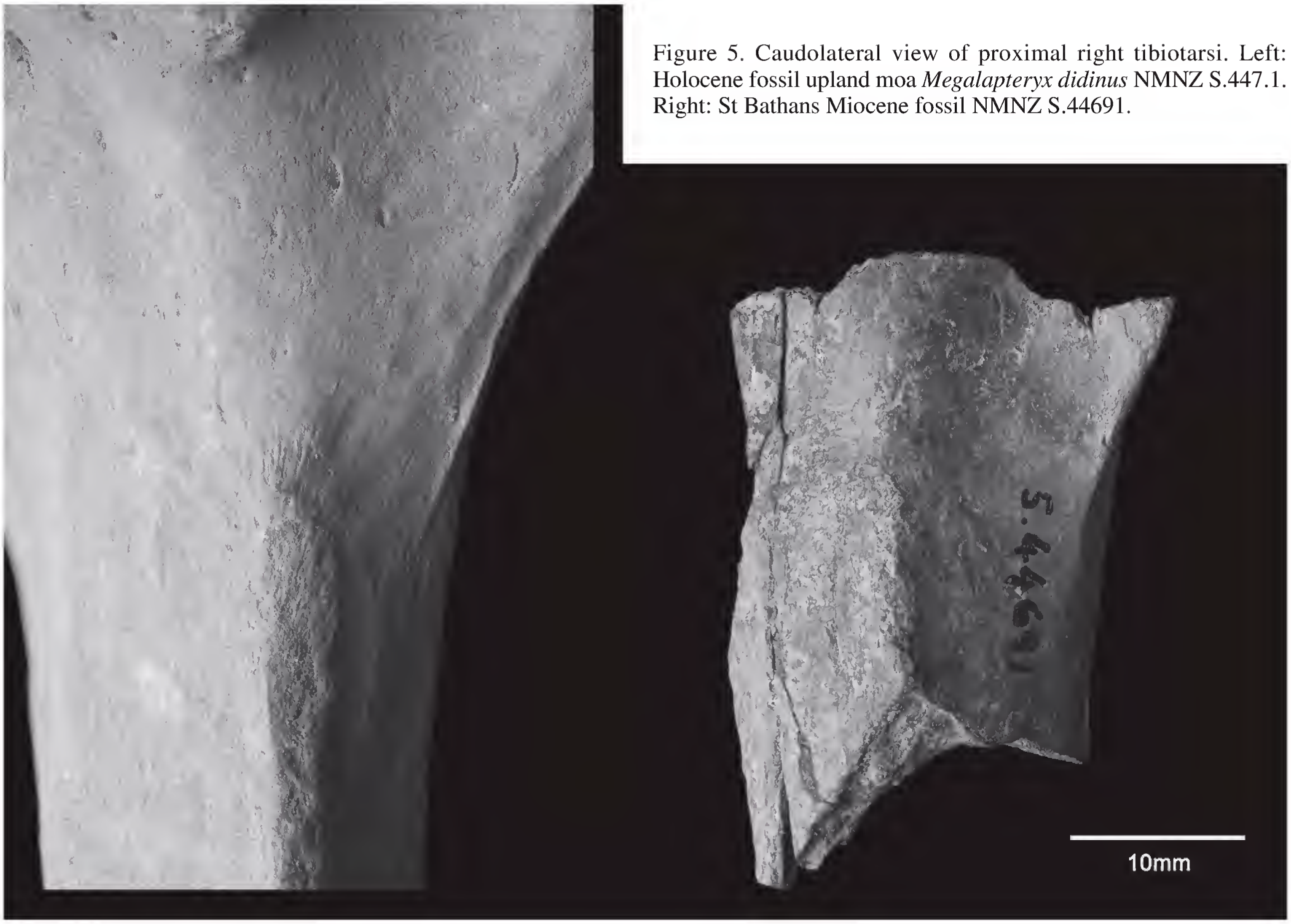

Figure 5. Caudolateral view of proximal right tibiotarsi. Left: Holocene fossil upland moa *Megalapteryx didinus* NMNZ S.447.1. Right: St Bathans Miocene fossil NMNZ S.44691.

Recent species but still sizable birds. Tantalisingly, there is one much thicker piece of fossil eggshell that presumably came from a moa weighing considerably more. Some moa were already enormous by the beginning of the Pleistocene 1.8 Ma (e.g., a giant moa *Dinornis*, represented by a femur NMNZ S.450; Marshall, 1919; Worthy *et al*., 1991). Large giant moa with femora of comparable size to this femur weighed 76–242 kg (Bunce *et al*., 2003). An algorithm for birds, based on NMNZ S.450 having a minimum femur shaft circumference of 198 mm (where mass in grams = $a.x^b$ and $a = -0.065$, x = minimum femur circumference, and $b = {}^{2.411}$; Campbell & Marcus, 1992, table 2), gives a mass of 224.0 kg for this animal. We therefore feel confident in debunking the stance of Goldberg *et al*. (2008) that "there is as yet no direct evidence… that their pre-Pleistocene ancestors were giants".

The large size of moa in the late Early Miocene (weighing somewhere between 20 and 242 kg) makes it likely that they were flightless, although proof of this is lacking. All Recent New Zealand bird taxa about 20 kg or larger were flightless (see Tennyson & Martinson, 2007).

If the ancestors of moa arrived in Zealandia after the Oligocene "drowning" 25–22 Ma by flying (Pole, 1994; Waters & Craw, 2006), then the new Miocene fossil finds reduce the time available for the colonization and the evolution of giant flightless forms to as little as three million years. Birds can become large and flightless within three million years (e.g., Trewick, 1997; Slikas *et al*., 2002) and, by itself, the St Bathans fossil evidence is insufficient to prove that moa had a pre-"drowning" origin in Zealandia. However, we have demonstrated that there is a much shorter time interval for this evolution to have occurred than previously known. The fact that moa are the only birds worldwide without even vestigial wing bones (Worthy & Holdaway, 2002) also suggests a very long history of flightlessness.

Although moa seem to have gone through a genetic bottleneck during the Oligocene marine transgression (Cooper & Cooper, 1995) and Recent lineages may have arisen only since the Late Miocene (Bunce *et al*., 2009), nearly all independent evidence indicates that moa diverged from their nearest relatives in the Paleocene or Cretaceous (at least 60 Ma) (e.g., Cooper *et al*., 2001; Cracraft, 2001; Haddrath & Baker, 2001; Grellet-Tinner, 2006; Phillips *et al*., 2010)—well before the Oligocene (34–24 Ma).

Another intriguing find of relevance to this debate is the presence of a probable divaricating plant in Early Miocene fossil lake sediments of central Otago (Campbell *et al*., 2000). This growth form is considered to have evolved as protection against moa feeding, with Lee *et al*. (2008) concluding that "New Zealand plants have been protecting themselves against moa browsing for at least the past 20 million years".

The St Bathans Fauna has provided the first glimpse of the land animals that were living in Zealandia after the Oligocene-Miocene submergence. Many characteristic Recent New Zealand taxa were present in the late Early Miocene 19–16 Ma but substantial changes have occurred subsequently resulting from both extinctions and colonizations (Worthy *et al*., 2009). Evidence of other "Gondwanan" vertebrate taxa in the St Bathans Fauna makes the total "drowning" theory even less likely: ancestors of New Zealand frogs, geckos (diplodactylines), tuatara, New Zealand wrens (Acanthisittidae) and the unusual ground-dwelling mammal would all have needed to colonize since the "drowning" (Jones *et al.*, 2009; Lee *et al.*, 2009; Worthy *et al.*, 2009, 2010) … and where would they have come from when there are no known Neogene source populations? In short, almost all archetypical Gondwanan terrestrial vertebrate taxa known from New Zealand's Recent fauna are now known to have had ancestors present in Zealandia in the late Early Miocene. If Zealandia was completely submerged, as Landis *et al.* (2008) and others contend, then all such taxa would need to have dispersed to Zealandia in as little as three million years and no such taxa would have arrived in the last 16 million years.

In addition to terrestrial vertebrates, numerous invertebrates, including hyriid freshwater mussels (Graf & Foighil, 2000), pettalid harvestmen (Boyer & Giribet, 2009), micropterigid moths, weta (Orthoptera) and freshwater crayfish (*Paranephrops* spp.) (Gibbs, 2006), and some plants (e.g., kauri *Agathis*; Stöckler *et al.*, 2002; Knapp *et al.*, 2007), also appear to be Gondwanan vicariants.

In summary, the traditional theory of some vicariant Gondwanan taxa surviving in the Recent fauna of New Zealand is supported by moa and other late Early Miocene (19–16 Ma) St Bathans fossils. Although the Zealandian continent was largely submerged from the Late Oligocene to the Early Miocene (about 25–22 Ma), there is increasing biotic evidence that some land must have remained. Moa appear to be an evolutionary phenomenon of much greater antiquity than "the past 23 million years" (contra Campbell & Landis, 2008) and "Moa's Ark" remains an appropriate epithet for New Zealand.

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Appendix 1

Thickness of "thick" Miocene eggshell from the St Bathans deposits (combined data from Worthy *et al.*, 2007 and new data).

NMNZ S.	site	no. of pieces	thickness (mm)
40935	Croc Site, layer 1	1	0.95
40936	Vinegar Hill	8	0.90 × 2, 1.00, 1.06, 1.10 × 4
40937.1	HH1b "riverbank"	1	0.86
40937.2	HH1b "riverbank"	1	1.68
40938.1–3	HH1b "riverbank"	1 (3 parts)	1.02
40938.4	HH1b "riverbank"	1	0.76
40938.5–8	HH1b "riverbank"	1 (4 parts)	1.08
40938.9	HH1b "riverbank"	1	1.02
40939	HH1b "riverbank"	1	1.12
42469	Croc Site, layer 1	1	0.91
42726	HH1a	1 (2 parts)	1.03
42822	HH1d	1	0.74
42936	Croc Site, layer 1	1	0.97
43159	HH1a	1	0.88
43210	HH2b/c	1 (2 parts)	0.90
44312	HH1b "riverbank"	37	0.68, 0.69 × 2, 0.70, 0.77 × 2, 0.79 × 2, 0.80 × 2, 0.82 × 2, 0.83, 0.84 × 2, 0.85, 0.86, 0.88 × 5, 0.89 × 3, 0.90 × 4, 0.91 × 2, 0.94 × 2, 0.96, 0.98, 1.01, 1.03
44343	HH1d	1 (4 parts)	1.14
44346	HH1d	1	1.04
44347	Between HH1a & HH1d	1 (4 parts)	1.13
44695	Vinegar Hill surface	1	0.91
44701	HH1a	1	1.00
44713	HH2	1	1.16
44766	HH1b "riverbank"	1	1.09
50292	HH1a	1	0.89
50181	HH1b "trench"	36	0.58, 0.71, 0.74 × 2, 0.77, 0.79, 0.84, 0.85, 0.86, 0.87, 0.88, 0.89 × 2, 0.90, 0.91, 0.92, 0.94 × 2, 0.95 × 2, 0.96 × 5, 0.97 × 5, 1.04, 1.07 × 2, 1.08 × 2, 1.19
50497	other side of valley from the main Vinegar Hill sites	1	1.00
50793	HH1d	1 (3 parts)	0.60
50687	Vinegar Hill, site 2	21	0.77, 0.79 × 2, 0.80, 0.84, 0.88, 0.91, 0.94, 0.95 × 2, 0.97, 1.02, 1.03 × 2, 1.04, 1.07, 1.08 × 2, 1.09, 1.10, 1.12
50820	HH1a	28	0.76, 0.77, 0.78, 0.85, 0.87, 0.88, 0.89, 0.90, 0.92, 0.95, 0.96 × 2, 1.02, 1.03, 1.04 × 5, 1.05, 1.07, 1.08 × 3, 1.09 × 2, 1.14, 1.15
		total = 154	mean thickness of 0.94 (±0.12 s.d.) mm (n = 153, excluding S. 40937.2)

Appendix 2

Data matrix of character-state distributions for eggshell characters of Recent palaeognaths.

List of characters based on Zelenitsky & Modesto (2003) and Grellet-Tinner (2006), including the character numbers used by them in brackets. Some of Grellet-Tinner's (2006) characters were not used for the following reasons: they could not be applied to eggshell fragments (characters 1 & 2); they were the same in all taxa scored here (characters 8, 11 & 12); or, after considering descriptions and figures in Tyler (1957), Tyler & Simkiss (1960), Silyn-Roberts & Sharp (1985), Mikhailov (1997) and Zelenitsky & Modesto (2003), seemed too variable to be useful (character 14). The data for elephant birds are based on Tyler & Simkiss (1960), Mikhailov (1997) and Grellet-Tinner (2006):

A (Zelenitsky & Modesto 59, Grellet-Tinner 10). EZ morphology:
    0 fine/porous, or
    1 blocky crystals.
B (Zelenitsky & Modesto 60). Composition of mammillae:
    0 poorly defined acicular wedges, or
    1 well-defined tabular wedges.
C (Zelenitsky & Modesto 61, Grellet-Tinner ?7). Mammillae proportions:
    0 wider than high, or
    1 higher than wide.
D (Zelenitsky & Modesto 62, Grellet-Tinner 5). Pore canals:
    0 unbranched, or
    1 branched/forked.
E (Zelenitsky & Modesto 63, Grellet-Tinner 3 and 4). Surficial ornamentation:
    0 present, or
    1 absent.
F (Zelenitsky & Modesto 65, Grellet-Tinner 9 and 13). Resistant zone (RZ) between the SZ and EZ:
    0 absent, or
    1 present.
G (Zelenitsky & Modesto 67). Vesiculation in MZ:
    0 present (strong), or
    1 absent (weak).
H (Grellet-Tinner 6). Surficial pore-depression:
    0 round, or
    1 slit-like.
I (Grellet-Tinner 15—we modified this character as descriptions and figures in Tyler (1957), Tyler & Simkiss (1960), Silyn-Roberts & Sharp (1985), Mikhailov (1997) and Zelenitsky & Modesto (2003) show that it is more variable than Grellet-Tinner (2006) presented). Ratio of EZ/SZ:
    0 greater than 0.2, or
    1 less than 0.2.

taxon	A	B	C	D	E	F	G	H	I
Tinamou	0–1	0	0	0	1	0	0	0	0[a]
Moa	1	1	1	1[b]	1	0	1	0–1[c]	1
Miocene fossils (thick)	1	1	1	1	1	0	1	0–1	1
Kiwi	1	0	1	0	1[d]	0	0	0	0
Cassowary	0	1	1	1	0	1	1	0	0
Emu	0	1	1	1	0	1	1	0	0
Ostrich	0	1	1	1	1	0	1	0	0–1
Rhea	0	1	1	1[b]	1	0	1	0–1[c]	1
Elephant bird	0	1	1	1[b]	0–1	0	1	1	1

[a] Grellet-Tinner (2006) considered tinamou to have an EZ/SZ ratio of 0.067 but Mikhailov (1997) and estimates from Grellet-Tinner (2006, fig. 21A) and Zelenitsky & Modesto (2003, fig. 1A) give a ratio > 0.2.

[b] Grellet-Tinner (2006) considered moa, rheas and elephant birds to have unbranched pore canals but clear branched/forked canals were detected by other workers (Tyler & Simkiss, 1960; Mikhailov, 1997; Zelenitsky & Modesto, 2003) in these taxa.

[c] Grellet-Tinner (2006) scored character H as 0 for rheas and 1 for moa but this varies within these groups (Gill, 2007, pers. obs.).

[d] We follow Zelenitsky & Modesto (2003) in considering kiwi to have an absence of surficial ornamentation (contrary to Grellet-Tinner, 2006).

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Regional Comparisons of the Thickness of Moa Eggshell Fragments (Aves: Dinornithiformes)

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ABSTRACT. Samples of moa eggshell fragments from eight sites throughout New Zealand were measured to investigate the usefulness of the graphed distribution of eggshell-thicknesses in reflecting the moa fauna of the site. Assuming larger moa species laid eggs with thicker eggshells, a frequency histogram of eggshell thicknesses for each site seems to mirror what is known (from bones) of the incidence and relative abundance of large and small moa species at the site. This is particularly so for North Island sites which had lower moa diversity than South Island sites. At North Cape and Tokerau Beach abundant thin eggshell (mode at 0.90–0.94 mm) was probably produced by *Euryapteryx* "*curtus-gravis*" and *Pachyornis geranoides*, and rarer thick eggshell (mostly 1.2–1.7 mm) by *Dinornis novaezealandiae*. At both Puketitiri and Castle Point there were broadly unimodal distributions of thin to medium-thickness eggshell, with thick eggshell almost absent. At Puketitiri the eggshell is assumed to be mainly from *Anomalopteryx didiformis*, and the slightly smaller *P. geranoides*, and averages thicker with a broader range than at Castle Point where the assumed identity of the eggshell lies with two small species (*P. geranoides* and *Eu. "curtus-gravis"*). At the four South Island sites the correlation to species is less clear. The modal thicknesses at Wairau Bar, Oamaru, Chatto Creek and Shag River are all in the range 1.15–1.44 mm and probably largely attributable to *Eu. "curtus-gravis"* which has a large form in the South Island and dominates the bones at all four sites. However, several other moas could have contributed the thinnest and thickest eggshells in most of the South Island samples. Archaeological sites had similar large ranges of eggshell-thickness to natural sites, suggesting that Maoris collected moa eggs from all available species and not just the largest ones. The study demonstrates the usefulness of eggshell-thickness histograms at particular sites as an adjunct to, or surrogate for, information on the relative abundance of moa bones, especially for North Island sites.

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Fossil bones and eggshell fragments are the main evidence of the former presence in New Zealand of moas (Dinornithiformes), the extinct large ratite birds currently thought to number 10 species (nomenclature after Worthy & Holdaway, 2002; Bunce *et al.*, 2003; Worthy, 2005). Moa eggshell fragments are common, often in large quantities, in various archaeological and Holocene fossil sites throughout New Zealand. However, there has been little research on the nature and characteristics of moa eggshell fragments, and reports of archaeological and paleontological excavations typically and unhelpfully record "moa eggshell", without further analysis. One aim of my recent work on moa eggs and eggshell (Gill, 2000, 2006, 2007) has been to seek a better understanding of unassociated, broken moa eggshell.

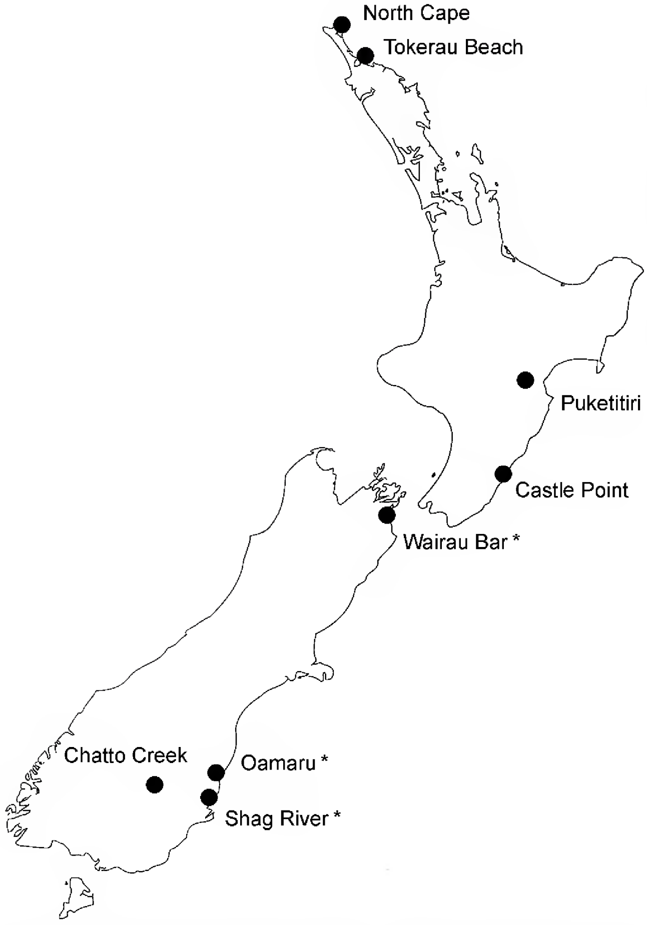


Figure 1. Locality map of New Zealand showing eight sites (four from each of North and South Islands) for which samples of moa eggshell fragments were measured in this study. Archaeological sites are marked with an asterisk (*).

It is well known that moa eggshell fragments vary in thickness, and differences between "thick" eggshell (ca. 1.3–1.7 mm) and "thin" eggshell (ca. 0.5–1.0 mm) were noted earlier (e.g., Archey, 1931). Thicker eggshell fragments presumably derive from larger eggs that were produced by the larger species of moas. Support for this comes from a general positive correlation between the lengths of whole moa eggs and their eggshell thicknesses (Gill, 2007: fig. 5). The moa fauna in a given region is a subset of the known species, and it follows that the thicknesses of the moa eggshell fragments at a fossil site should reflect the sizes, and thus identities, of the resident species of moa. The relative abundance of eggshell of different thicknesses at a site might also reflect the relative abundance of the species that produced them.

The aim of this study was to analyze the thickness of moa eggshell fragments at a range of sites and look for agreement between the thickness profiles and the diversity and relative abundance of the moa species at the sites as determined from bones. It was a test of the notion that a histogram of thicknesses taken from a large sample of eggshell fragments at a site gives a profile reflective of moa composition at the site.

Materials and methods

Sites. I examined samples of moa eggshell fragments at eight sites or geographic areas chosen because they had yielded large samples held in museum collections, and the sites were spread latitudinally throughout New Zealand (Fig. 1). Five are natural sites, known (or assumed) to be of Holocene age, i.e. no older than 10,000 years before present. Three archaeological sites, all in the South Island, are assumed to date from within 100–200 years of first human settlement of New Zealand (which was ca. 1250 A.D.; Anderson, 1991; Wilmshurst *et al.*, 2008). The sites were as follows (see Table 3 for latitudes and sample sizes; see Appendix for museum registration numbers):

- *North Cape, Northland* (natural sites)
- *Tokerau Beach, Northland* (natural sites; same sample analysed in Gill, 2000)
- Puketitiri, Hawke's Bay (natural sites)
- *Castle Point region, Wairarapa Coast* (natural sites)
- *Wairau Bar, Marlborough* (archaeological site)
- *Oamaru, North Otago* (archaeological site)
- *Chatto Creek, Central Otago* (natural sites)
- *Shag River mouth, Otago* (archaeological site)

Samples. Eggshell fragments from the selected sites were examined closely and any with significant signs of surface-wear were rejected. For each acceptable fragment (n = 3565), one measurement of eggshell thickness was made to the nearest 0.01 mm (with vernier callipers or a screw micrometer) at an undamaged point on the edge of the fragment. Thicknesses were plotted as histograms with 0.05 mm intervals to give a very finely-divided spread of thickness classes (0.50–0.54, 0.55–0.59, 0.60–0.64 etc.). All fragments were white (or shades close to white) except for six of the 79 fragments in OM AV7477, which were green. Green eggshell belongs to *Megalapteryx didinus* (see Gill, 2007), but the identity of white eggshell is open to conjecture.

Moa faunas. The moa faunas at each site are known from the identity and relative abundance of bones. The taxonomy and nomenclature of moas is still under review. Bunce *et al.* (2003) showed that instead of three species of giant moas *Dinornis* throughout New Zealand there is just one North Island species (*D. novaezealandiae*) and one South Island species (*D. robustus*). This has simplified the moa fauna at most sites. Worthy (2005) showed that the stout-legged moa, previously called *Euryapteryx geranoides*, should now be called *Eu. gravis*, and that Mappin's moa *Pachyornis mappini* is now *P. geranoides*.

It is also likely that *Eu. gravis* (North and South Islands) and *Eu. curtus* (North Island only) are conspecific, with size-differences in the bone samples reflecting various combinations of temporal, geographic and sexual variation (Tennyson & Martinson, 2006: 36, 146; T.H. Worthy, pers. comm. 2008). For example, *Eu. gravis* is recorded from Tokerau Beach but such bones probably belonged to the biggest of the larger (female) individuals of *Euryapteryx* at that site. Worthy (1987) showed that histograms of bone-lengths of *Euryapteryx* from Tokerau Beach were all bimodal, and he considered the different size-classes to reflect sexual dimorphism. The Holocene bones of *Euryapteryx* vary clinally in size, tending larger towards the south (Worthy, 1987). The two nominal species are referred

Table 1. Presumed relative abundance of moa taxa (based on bones) at North Island sites where eggshell thickness was assessed. ••• predominant, •• present, • rare, — absent.

	Euryapteryx	*P. geranoides*	*A. didiformis*	*D. novaezealandiae*
North Cape	•••	••	—	•
Tokerau Beach	•••	•	—	•
Puketitiri	—	••	•••	•
Castle Point	•••	•••	••	••

Table 2. Presumed relative abundance of moa taxa (based on bones) at South Island sites where eggshell thickness was assessed. ••• predominant, •• present, • rare, — absent.

	Euryapteryx	*P. elephantopus*	*A. didiformis*	*E. crassus*	*M. didinus*	*D. robustus*
Wairau Bar	•••	•	•	••	•	•
Oamaru	•••	••	?	••	?	?
Chatto Creek	•••	••	—	••	••	••
Shag River	•••	•	—	••	—	••

to here together as *Eu. "curtus-gravis"*. Tables 1 and 2, and the following notes, summarize the Holocene moa faunas at the sites in this study.

North Cape. The most abundant moas were *Euryapteryx "curtus-gravis"* and *Pachyornis geranoides*, while *Dinornis novaezealandiae* was rarer (Atkinson & Millener, 1991). Evidence from bones is that *P. geranoides* was nearly as common as *Eu. "curtus-gravis"*.

Tokerau Beach. About 95% of skeletons in the area are *Eu. "curtus-gravis"* (Worthy & Holdaway, 2002: 184). Rarer species at the site (evidence discussed by Gill, 2000) were *P. geranoides* and *D. novaezealandiae*.

Puketitiri. *Anomalopteryx didiformis* was the main moa found at caves and rock-shelters of inland Hawke's Bay, closely followed by *P. geranoides*, with *D. novaezealandiae* rarer (Worthy & Holdaway, 2000).

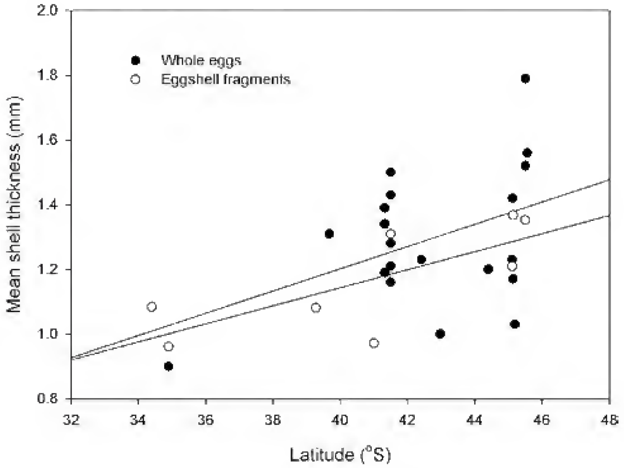


Figure 2. Regressions of mean eggshell thickness on latitude for the eight geographic samples in this study (Table 3) and for the 20 whole moa eggs for which measurements of eggshell thickness are possible (Gill, 2007). For eggshell fragments (open circles), the four North Island data-points are at bottom left and the four South Island ones at middle right. The regression lines and correlation coefficients are: y = 0.028x + 0.027, r = 0.75 (fragments; lower line); y = 0.034x–0.17, r = 0.44 (whole eggs; upper line).

Castle Point. *Pachyornis geranoides* and *Eu. "curtus-gravis"* were co-dominant in the area with lesser numbers of *A. didiformis* and *D. novaezealandiae* (T.H. Worthy, pers. comm. 2008). The moa fauna was therefore very like that at North Cape.

Wairau Bar. *Euryapteryx "curtus-gravis"* predominated with lesser numbers of *Emeus crassus* and rare examples of *A. didiformis, Megalapteryx didinus, Pachyornis elephantopus* and *Dinornis robustus* (Scofield *et al.*, 2003).

Oamaru. *Euryapteryx "curtus-gravis"* dominated and *P. elephantopus* was much less common (Worthy & Holdaway, 2002: 181). *Emeus crassus* was present (Trotter, 1970).

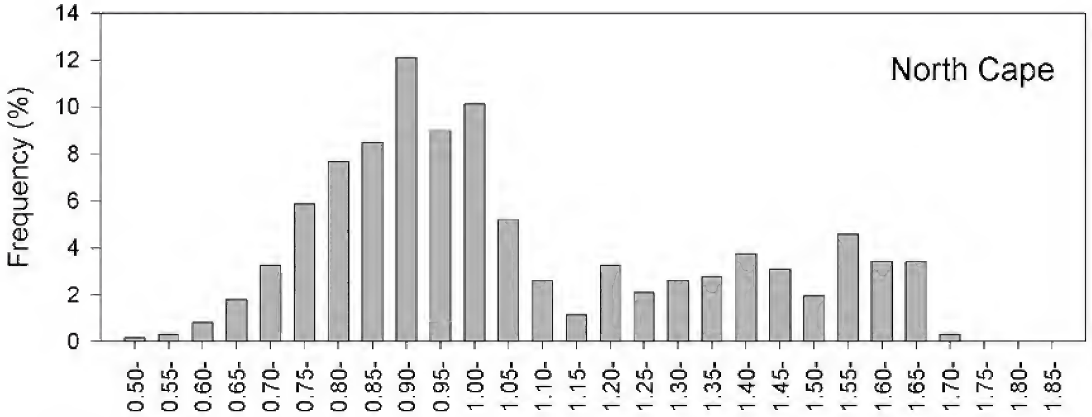
Chatto Creek. In the Central Otago area *Eu. "curtus-gravis"* was the dominant moa, with lesser numbers of *P. elephantopus, Em. crassus, M. didinus* and *D. robustus* (Worthy, 1998).

Shag River. *Euryapteryx "curtus-gravis"* was the dominant moa with lesser numbers of *Em. crassus* and *D. robustus* (Anderson *et al.*, 1996).

Results

Table 3 summarizes thickness for the samples of eggshell fragments at the eight sites in this study, and for whole moa eggs, and shows that minimum, mean and maximum thicknesses tend to be higher for South Island than for North Island samples. Fig. 2 shows the relationship between mean thickness and latitude for the eight broken eggshell samples (open circles). The eggshell thicknesses of whole eggs (Fig. 2; closed circles) show a very similar regression to the eggshell fragments, though data for the North Island are few.

Figures 3–10 show the histograms of moa eggshell thickness for each of the eight sites. North Cape (Fig. 3) and Tokerau Beach (Fig. 4) show a similar pattern—a broadly bimodal distribution with a spread of numerous thin eggshell fragments (mode at 0.90–0.94 mm) and a second spread of rarer thicker fragments (mostly 1.2–1.7 mm thick). The thin eggshell was presumably produced by *Euryapteryx "curtus-gravis"* with a lesser contribution by *Pachyornis geranoides*. Both are small moas, and the former is particularly small in the north (Worthy, 1987). The latter species would have had a



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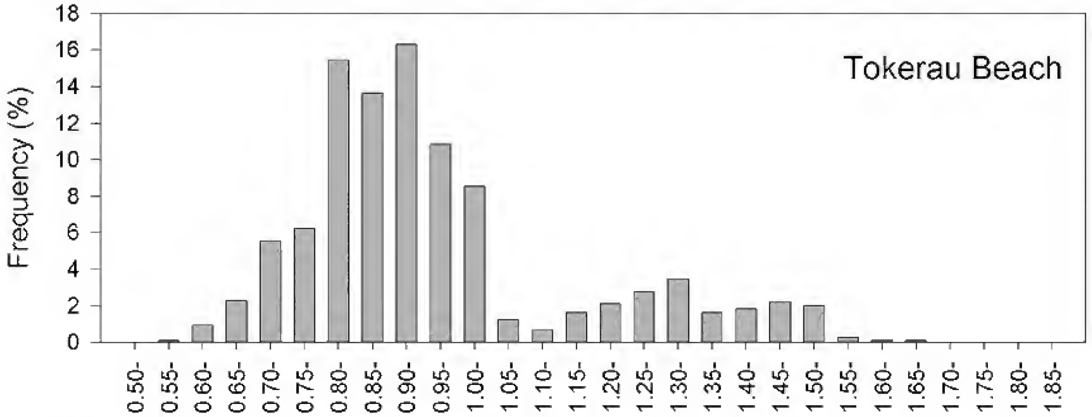

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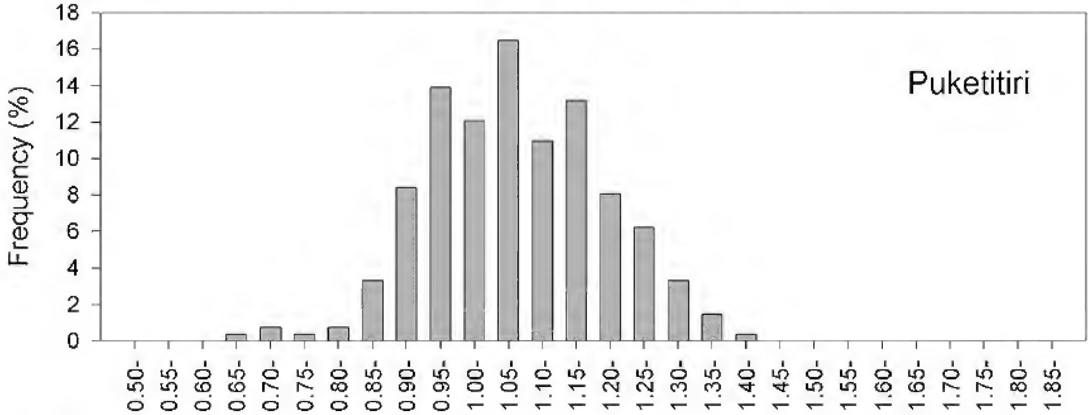

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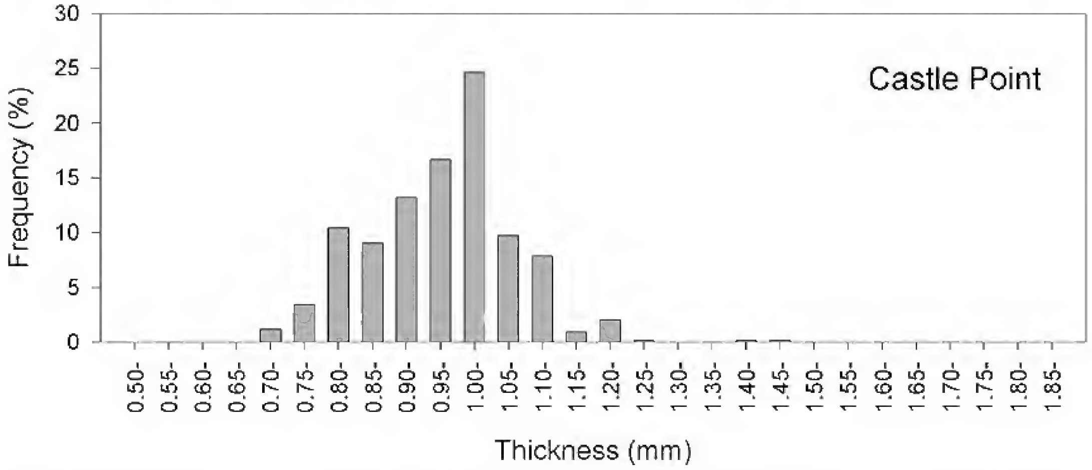

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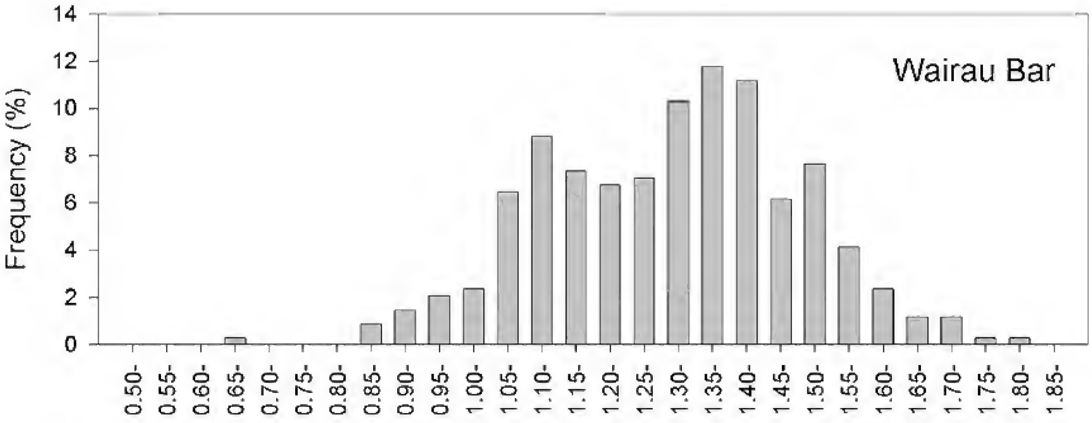
Figures 3–6. Histograms of moa eggshell thicknesses for samples of (Fig. 3) 612 fragments from North Cape, Northland; (Fig. 4) 1042 fragments from Tokerau Beach, Northland; (Fig. 5) 273 fragments from Puketitiri, Hawke's Bay; and (Fig. 6) 431 fragments from Castle Point, Wairarapa.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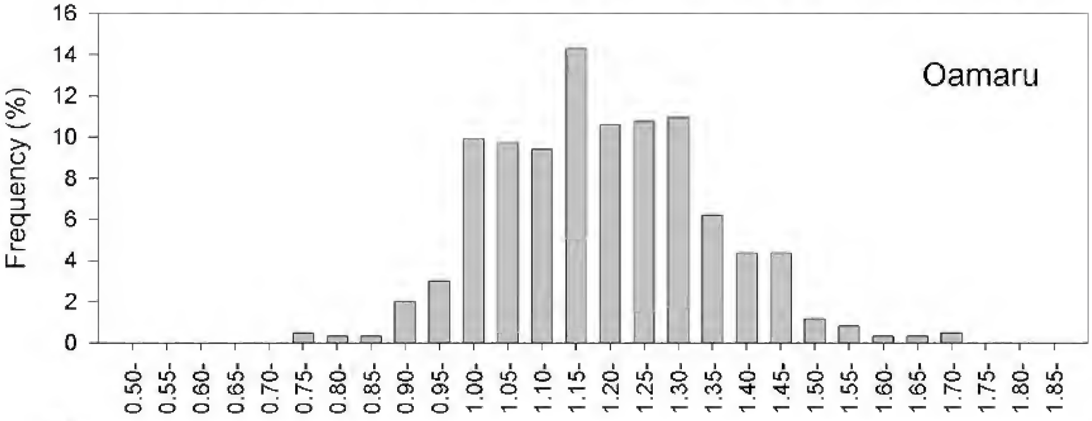
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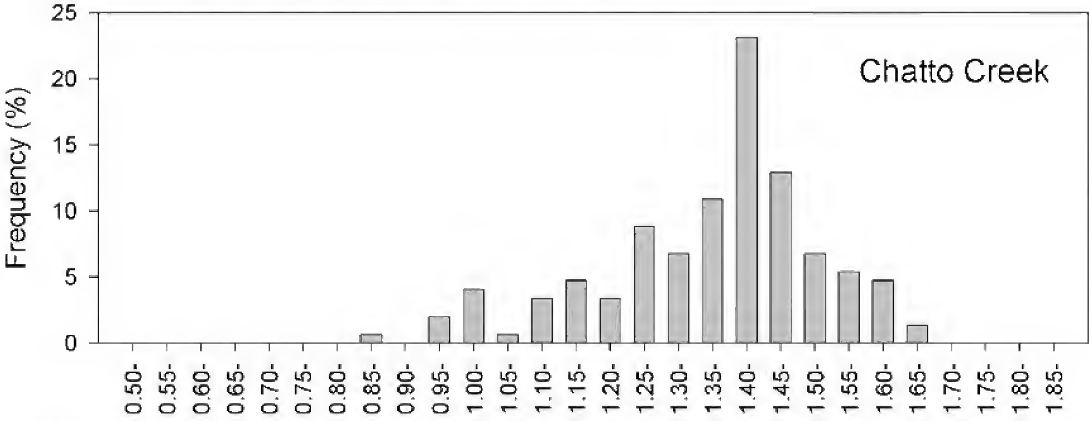
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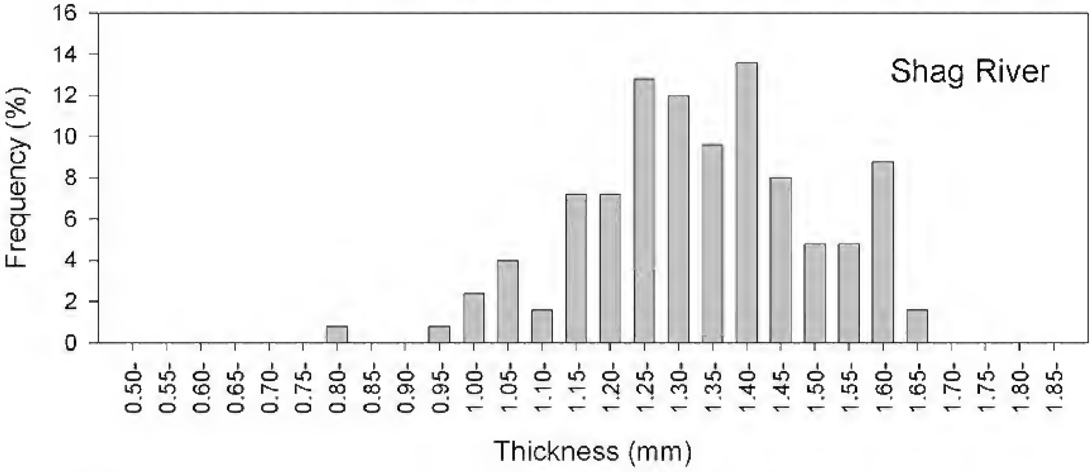
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Figures 7–10. Histograms of moa eggshell thicknesses for samples of (Fig. 7) 340 fragments from the Wairau Bar archaeological site, Marlborough; (Fig. 8) 595 fragments from the Oamaru archaeological site; (Fig. 9) 147 fragments from Chatto Creek, Central Otago; and (Fig. 10) 125 fragments from the Shag River archaeological site, Otago.

Table 3. Latitude (°S) and descriptive statistics for eggshell thickness (mm) for samples of moa eggshell fragments from eight sites around New Zealand (Fig. 1). In brackets after range is the arithmetic extent of the range (mm), i.e. maximum minus minimum. Maximum and minimum eggshell thicknesses (mm) for the North and South Islands (overall) are shown for the samples of eggshell fragments in this study, and for the whole eggs for which eggshell thicknesses can be measured (Gill, 2007).

locality	mean	n	s.d.	range	latitude
North Island					
North Cape	1.08	612	0.287	0.54–1.71 (1.17)	34.4
Tokerau Beach	0.96	1042	0.210	0.56–1.69 (1.13)	34.9
Puketitiri	1.08	273	0.129	0.65–1.41 (0.76)	39.3
Castle Point	0.97	431	0.109	0.70–1.48 (0.78)	41.0
fragments (overall)				0.54–1.71	
whole eggs				0.90–1.50	
South Island					
Wairau Bar	1.31	340	0.188	0.66–1.82 (1.16)	41.5
Oamaru	1.21	595	0.156	0.77–1.73 (0.96)	45.1
Chatto Creek	1.37	147	0.161	0.89–1.65 (0.76)	45.1
Shag River	1.35	125	0.167	0.83–1.69 (0.86)	45.5
fragments (overall)				0.66–1.82	
whole eggs				1.02–1.89	

minor contribution at Tokerau Beach and a greater contribution at North Cape, according to the relative abundance of bones at these sites, but the eggshells of the two species seem inseparable in the histograms. The thick eggshell at the two northern sites (Figs. 3, 4) was presumably produced by *Dinornis novaezealandiae*, the only large moa present.

Puketitiri (Fig. 5) and Castle Point (Fig. 6) show broadly unimodal thickness histograms of thin to medium-thickness eggshell, with thick eggshell almost absent. At Puketitiri the eggshell is assumed to be mainly from the small species *Anomalopteryx didiformis* and the even smaller *P. geranoides*. At Castle Point the assumption is that the eggshell is a mixed sample attributable largely to *P. geranoides* and *Eu. "curtus-gravis"*, as at North Cape and Tokerau Beach. Indeed, the frequency distribution at Castle Point, with a mode at about 1.0 mm, is very like that of thin eggshell at the two northern-most sites. *Anomalopteryx didiformis* probably had thicker eggshell than *P. geranoides*, being larger, and this may be reflected in the thicker eggshell overall at Puketitiri than at Castle Point. Some of the thickest eggshell at Puketitiri, and the few pieces in the 1.40–1.49 mm range at Castle Point, may belong to *Dinornis*.

The four South Island samples are all broadly unimodal and towards the thicker end of the spectrum. Very thin eggshell is rare. The modal thicknesses at Wairau Bar (Fig. 7), Chatto Creek (Fig. 9) and Shag River (Fig. 10) are all at 1.35–1.44 mm. Oamaru (Fig. 8) has a lower mode (1.15–1.19 mm) but greater modal thickness than for the two North Island unimodal samples (Puketitiri and Castle Point). *Eu. "curtus-gravis"* dominated the bones at all four South Island sites, and much of the eggshell presumably belongs to this moa, which is large-statured in the South Island.

However, the South Island situation is compounded by a greater diversity of moas at each site (usually 4–6 spp.; Table 2) than in the North Island (3–4 spp.; Table 1). *Emeus crassus, Anomalopteryx didiformis* and *Megalapteryx didinus* could have contributed the thinnest eggshells in most of the South Island samples, and *Pachyornis elephantopus* and *Dinornis robustus* were present at most sites to contribute the thickest eggshell fragments.

A few fragments from Chatto Creek (4%) were green, i.e. attributable to *M. didinus*, and all were 0.89–1.13 mm thick, placing them at the very left-hand tail of the histogram (Fig. 9). White eggshell in that thickness range was also present, which at Chatto Creek could be *Megalapteryx* eggshell that has faded to white (see Gill, 2007), or attributable to *E. crassus*.

North Cape and Tokerau Beach have larger ranges of eggshell thicknesses (1.17 mm, 1.13 mm; Table 3) than all other sites except Wairau Bar (1.16 mm; Table 3). However, the thickness range at Wairau is exaggerated by one outlying thin fragment in the 0.65–0.69 mm range (Fig. 7) which could conceivably belong to a large bird other than a moa.

Discussion

The latitudinal trend in moa eggshell thickness, with thicker eggshells in the south (Fig. 2), has two probable explanations. One underlying factor will be the presence of certain large moa species in the South Island (most notably *Pachyornis elephantopus*) that are absent in the North Island. However, Bergmann's Rule may also be involved. For New Zealand birds, this predicts that where a species varies geographically in size, individuals in cooler (e.g., southern) areas will be larger. Bergmann's Rule is thought to have operated in Holocene populations of various moas, e.g., *Euryapteryx* (Worthy, 1987, 1992) and *Dinornis* (Worthy *et al.*, 2005), whose populations are present in both islands. If the birds of these species varied clinally in body-size, then so too may the size of their eggs and the thickness of their eggshells.

In general, the histograms of moa eggshell thickness seem to mirror closely what is known of the diversity and relative abundance of moas at the sites. For example, the bimodally distributed thick and thin eggshell at the two northern-most sites (Figs 3, 4) seem to fit with the indication from bones of numerous small moas (*Euryapteryx "curtus-gravis"* and *Pachyornis geranoides*) and rarer large moas (*Dinornis novaezealandiae*). The extreme spread of eggshell thicknesses at each of the two northernmost sites must reflect the presence there of moas of extreme sizes—the smallest known members of the *Euryapteryx "curtus-gravis"* complex and a *Dinornis*. The situation is now much simpler and clearer than when three species of *Dinornis* and two of *Euryapteryx* were thought to occur at Tokerau Beach (Gill, 2000).

We can infer from the histograms that both *Euryapteryx "curtus-gravis"* and *Pachyornis geranoides* had eggshell roughly 0.5–1.2 mm thick at North Cape (Fig. 3) and 0.6–1.1 mm at Tokerau Beach (Fig. 4). A whole egg from Tokerau Beach thought to belong to *Eu. "curtus-gravis"* (Gill, 2006: Egg 2) has eggshell about 0.9 mm thick (Archey, 1931), which places it at the mode in both thickness histograms and in the centre of the spread of thin eggshell fragments. The same histograms suggest that the eggshell of *Dinornis novaezealandiae* was approximately 1.1–1.7 mm thick but there is no information from whole eggs on eggshell thickness in this species. The largest North Island egg (Gill, 2006: Egg 5, Waitomo) is probably *Dinornis* but the eggshell fragments are assembled in a way that prevents their thickness being measured. The thickest eggshell measured from North Island whole eggs is only 1.5 mm (Table 3) and was attributed to *Anomalopteryx* (Gill, 2006: Egg 8).

We can predict from Fig. 5 (Puketitiri) that *P. geranoides* had eggshell from about 0.7 mm thick to an unknown maximum, and that *A. didiformis* at the same site had eggshell from an unknown minimum to 1.4 mm thick. No whole eggs of *P. geranoides* are known but four whole eggs from inland North Island sites and most likely attributable to *A. didiformis* have data on eggshell thickness (Gill, 2006, 2007: Eggs 7, 8, 13 and 14). The attribution of the eggs to *Anomalopteryx* is based on that small species dominating at the inland sites where the eggs were found and on the eggs being small (i.e. 152–175 mm long). Thirty-five eggshell thickness measurements from these four eggs had a range of 1.1–1.5 mm. This supports the notion that at least the thicker eggshell at Puketitiri belonged to *A. didiformis*. By elimination, much of the thinner eggshell at Puketitiri, especially in the range 0.7–1.0 mm, must belong to *P. geranoides*. At Castle Point, where the small and similarly-sized *P. geranoides* and *Eu. "curtus-gravis"* dominated (on bone evidence), most of the eggshell was indeed in that range (Fig. 6).

Given that the large South Island form of *Eu. "curtus-gravis"* dominated the bones at all four South Island sites, the frequency bars in the histograms suggest that its eggshell was about 1.1–1.5 mm thick at Wairau Bar (Fig. 7), 1.0–1.3 mm at Oamaru (Fig. 8), 1.3–1.5 mm at Chatto Creek (Fig. 9) and 1.2–1.6 mm at Shag River (Fig. 10), or roughly 1.0–1.6 mm for the South Island in general. Considering whole eggs, there are seven South Island eggs possibly attributable to *Euryapteryx* (Gill, 2006, 2007): Eggs 16 and 18–21 from the same Wairau Bar site as the eggshell fragments (Fig. 7) and Eggs 11 and 32 from the same Oamaru site as in Fig. 8. These eggs are not objectively linked to *Euryapteryx*, but they are medium-sized (i.e. 194–215 mm long) and assumed to belong to the medium-sized moa that dominates bones at the sites. Fifty-three thickness measurements from these seven eggs had a range of 1.1–1.7 mm. This close agreement in thickness between the broken eggshell and whole eggshells reinforces the conjecture that the bulk of the eggshell fragments at Wairau Bar, Oamaru, Chatto Creek and Shag River are from medium-sized eggs that were probably *Euryapteryx*.

Green eggshell fragments at Chatto Creek were thin (0.89–1.13 mm) and signal the presence of *Megalapteryx didinus*. Three whole green eggs, two from Chatto Creek (Gill, 2006: Eggs 22 and 23) and one from Mt Aspiring National Park (Egg 29), had similarly thin eggshell (1.1–1.2 mm thick; Gill, 2007). A whole egg from the Shag River site has an eggshell-thickness of 1.73–1.89 mm (Gill, 2007: Egg 27), the thickest moa eggshell ever recorded, and thought to belong to *P. elephantopus*. This extreme thickness was not represented in the broken eggshell sample from that site (Fig. 10); the sample of 125 fragments was clearly not large enough. However, the Shag River sample has a big peak at 1.60–1.64 mm, more so than for any other sample. These thickest fragments in the Shag River sample may be attributable to *P. elephantopus*.

The archaeological eggshell samples at Wairau Bar, Oamaru and Shag River are presumably biased towards the moa eggs that local Maoris collected and discarded. Yet the range of eggshell thicknesses at these midden sites is very large, and seems no different from the range of thicknesses at natural sites (Table 3). This suggests that moa eggs of all available sizes (i.e. from all available species) were collected for human use, not just the largest ones.

This study suggests a usefulness in histograms of moa eggshell thicknesses generated for specific paleontological and archaeological sites. Moa eggshell thickness profiles seem broadly to reflect the moa faunas at the sites, and may be a helpful adjunct to, or surrogate for, information on the relative abundance of moa bones at sites. This is especially so in the North Island where moas are usually less diverse at a site than in the South Island.

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Appendix

Museum registration numbers of the samples from which moa eggshell fragments were measured for thickness (number of fragments measured shown in brackets). Where the number measured was not the entire sample, fragments were chosen at random. Museum codes: *UO*, Anthropology Department, University of Otago, Dunedin; *AIM*, Auckland Museum, Auckland; *CMC*, Canterbury Museum, Christchurch; *HBM*, Hawke's Bay Museum, Napier; *NMNZ*, Museum of New Zealand Te Papa Tongarewa, Wellington; *OM*, Otago Museum, Dunedin.

North Cape (24 samples, 612 fragments). Samples collected 1976–1999 by F.J. Brook, N. Douglas, B.J. Gill, R. Renwick and H. Seelye.—*Tom Bowling Bay* (22 samples, 591 fragments). AIM LB6774 (1), LB6775 (7), LB7930 (81), LB7931 (39), LB7932 (27), LB7933 (16), LB7934 (16), LB7935 (31), LB7937 (30), LB8487 (23), LB8488 (4), LB8510 (65), LB8511 (4), LB8862 (5), LB8863 (29), LB9223 (8), LB9224 (1), LB9226 (27), LB9227 (37), LB9228 (34), LB9230 (39), LB9231 (67).—*Waikuku Beach* (2 samples, 21 fragments) AIM LB7936 (18), LB8825 (3).

Tokerau Beach (97 samples, 1,042 fragments). See Gill (2000: Appendix 1).

Puketitiri (5 samples, 273 fragments). Samples collected 1950s to 1961 by W.H. Hartree and J.C. Yaldwyn. In separate labelled containers at HBM; not registered or numbered. "Bush Face No. 1" (140), "Hukanui No. 7b 1959–1960" (25), "Hukanui No. 7b May 1960" (40), Hukanui No. 7b (cigarette tin) (60), Hukanui No. 7b (another cigarette tin) (8).

Castle Point (11 samples, 431 fragments). Samples collected 1934–2000 by E. Barton, T. Cairns, I. Cameron, I. Dandermam, E. Smith and A.J.D. Tennyson.—*Coast between Mataikona and Whakataki* NMNZ S23166 (52), S23167 (15), S36733 (3), S37890 (20), S37910 (13), S37913 (92), S37923 (23), S38403 (97), S38441 (56), S38460 (10), S40676 (50).

Wairau Bar (23 samples, 340 fragments). Archaeological excavations by J.R. Eyles, R. Duff, R. Perano and Canterbury Museum Archaeological Society 1942–1959. CMC AV19947 (4), AV19948 (50), AV19951 (20), AV19960 (25), AV19966 (27), AV19968 (7), AV19971 (22), AV19974 (10), AV19978 (13), AV19979 (12), AV19981 (16), AV19986 (6), AV19987 (35), AV19990 (6), AV20038 (8), AV21128 (27), AV21129 (10), AV21137 (5), AV21167 (28), AV25620 (1), AV25882 (1), AV29513 (4), AV29528 (3).

Oamaru (23 samples, 595 fragments). Archaeological excavations by W.B.D. Mantell ca. 1852.

The Mantell collection at AIM (LB4014) is a large assemblage of eggshell fragments believed to have been collected from a Maori midden site at Awamoa, near Oamaru, North Otago (Archey, 1941: 74). Mantell grouped the fragments on some basis. Within each group, numerous fragments are joined in an attempt to reconstruct sections of the original eggs, but thickness varies greatly within most of these groupings so they cannot represent separate individual eggs.

Boxes A–D (20), Box E (1), Boxes F–G (2), Box H (56), Box I (23), Boxes J-K (20), Box L (17), Boxes M-N (23), Box O (21), Box P (17), Box Q (20), Box R (30), Box S (27), Box 4014/1 (56), Box 4014/2 (43), Box 4014/3 (92), Box 4014/4 (22).

Chatto Creek (2 samples, 147 fragments). Samples collected ca. 1954 (collector not recorded). OM AV7376 (68), AV7477 (79).

Shag River (2 samples, 125 fragments). Archaeological excavations led by A. Anderson 1988–1989. UO SM/B (23), SM/C (102).

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A New Genus for the Extinct Late Pleistocene Owl *Strix brea* Howard (Aves: Strigiformes) from Rancho La Brea, California

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ABSTRACT. We review all of the fossil specimens from the upper Pleistocene Rancho La Brea asphalt deposits previously referred to the extinct owl *Strix brea*, and all newly identified specimens referable to that species. This review and emended description of *Strix brea* have provided a clearer picture of this species, and we find that it is more appropriately placed in a new genus, *Oraristrix*, whose affinities remain unclear. We provide a variety of morphometric data and more detailed osteological descriptions of this extinct owl based on 138 specimens from the Rancho La Brea collections in the George C. Page Museum that represent a minimum of 23 individuals. An additional nine specimens of this extinct species were confirmed in collections from the upper Pleistocene asphalt deposits of Carpinteria, California. *Oraristrix brea* is interpreted as being more terrestrial in habits than forest owls because, compared to available species of the genera *Bubo* and *Strix*, it had longer legs relative to its wingspan.

CAMPBELL JR., KENNETH E., & ZBIGNIEW M. BOCHEŃSKI, 2010. A new genus for the extinct Late Pleistocene owl *Strix brea* Howard (Aves: Strigiformes) from Rancho La Brea, California. In *Proceedings of the VII International Meeting of the Society of Avian Paleontology and Evolution*, ed. W.E. Boles and T.H. Worthy. *Records of the Australian Museum* 62(1): 123–144.

A large, extinct owl from the upper Pleistocene asphalt deposits of Rancho La Brea, California was described as *Strix brea* Howard, 1933. In addition to the holotypic tarsometatarsus, several other elements of the skeleton were briefly described and referred to this species by Howard (1933). However, since its original description, with the exception of being included in faunal lists (e.g., Howard, 1962), this species, which is known as the Brea Owl, has not been revisited. Herein we reevaluate the characters Howard (1933) used to distinguish the species, describe additional characters, illustrate bones not previously illustrated, and add to the list of elements and specimens referable to this extinct species. We offer suggestions as to the size and life habits of the Brea Owl based on its osteology and limb bone proportions. *Strix brea* is found to be a valid species, but one best placed in a new genus.

This study is part of an overall review of all of the fossil owls in the collections from Rancho La Brea maintained at the George C. Page Museum by the Natural History Museum of Los Angeles County (LACM). At least nine species of owls are represented in the collections by a total of over 7500 specimens. In the course of this review we found that the post-cranial elements of the genera of owls could be fairly easily distinguished by osteological characters, at least for the several genera represented in the Rancho La Brea collection. This finding is contrary to that of Olson & James (1991), who, citing an unpublished work by Ford (1967), suggested that post-cranial differences between the various subgroups and genera of owls are very slight or non-existent.

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Materials and methods

The fossil specimens were compared in detail with specimens of modern *Bubo virginianus* (20+) and all of the numerous fossil specimens of *B. virginianus* from Rancho La Brea, *B. bubo* (4), *B. africanus* (1), *Strix occidentalis* (8), *S. varia* (7), *S. nebulosa* (9), and *S. aluco* (3). The numbers reflect the largest sample sizes of each species available for comparison. Points on scatter diagrams are often less numerous because of incomplete modern comparative specimens. The genera *Ketupa* and *Nyctea* are considered by some (Amadon & Bull, 1988; Wink & Heidrich, 1999; Wink *et al*., 2008) as properly being included within *Bubo*, so these genera were included in our study. *Nyctea*, for the most part, agrees with *Bubo* as far as the osteological characters useful for distinguishing the Brea Owl from *Bubo* and *Strix* are concerned. *Ketupa* [*K. ketupa* (1), *K. zeylonensis* (3)], on the other hand, varies considerably from *Bubo* osteologically, and we find it to be easily distinguished from both *Bubo* and the Brea Owl. In our opinion, based on its osteological features, we agree with Sibley & Monroe (1990) that *Ketupa* is a valid genus separate from *Bubo*. However, we were unable to compare the species of *Ketupa* with those Asian species of *Bubo* that Wink & Heidrich (1999) and Wink *et al*. (2008) suggested were closest to *Ketupa* based on molecular studies.

Similarly, the genus *Ciccaba* is considered by some as properly being included within *Strix* (e.g., Sibley & Monroe, 1990; Wink & Heidrich, 1999; Wink *et al*., 2008), and we found that two species referred to *Ciccaba* [*C. virgata* (1) and *C. nigrolineata* (1)] agree with *Strix* as far as most of the osteological characters we detail below are concerned. Based on the osteology of available specimens, we accept that *Nyctea* belongs within *Bubo* and *Ciccaba* within *Strix*. Comparisons were also made with the genera *Tyto, Otus, Megascops, Lophostrix, Pulsatrix, Surnia, Glaucidium, Athene, Aegolius, Micrathene, Ninox*, and *Asio*. Each of these genera can be readily distinguished from *Bubo, Strix*, and the Brea Owl using osteological characters. In molecular studies, *Strix* and *Bubo* appear as closely related taxa (Wink & Heidrich, 1999; Wink *et al*., 2008), which is reflected in the many osteological characters they share that differ significantly from those of the other genera examined. Therefore, because this study was not intended as a comparative osteological review of all genera of owls we limit our detailed comparisons to species of *Bubo* and *Strix*, the genera that most closely resemble the Brea Owl osteologically.

Measurements were taken using digital calipers accurate to 0.01 mm, and all data were captured directly to computer. The measurements were stored, and the basic statistics, including minimum, maximum, arithmetic mean, and standard deviations, were computed in Microsoft Excel. For illustrations as to how the measurements were taken, see Appendix 2. All bones were checked for ratios useful for differentiating the species, and scatter diagrams of the ratios were prepared using Microsoft Excel and Corel Photo-Paint. Osteological terminology is primarily from Baumel & Witmer (1993). Abbreviations used: *Cond*. = condylus; *Fac. artic*. = facies articularis; *Lig. coll*. = ligamentum collaterale; *Proc*. = processus; *Tub*. = tuberulum

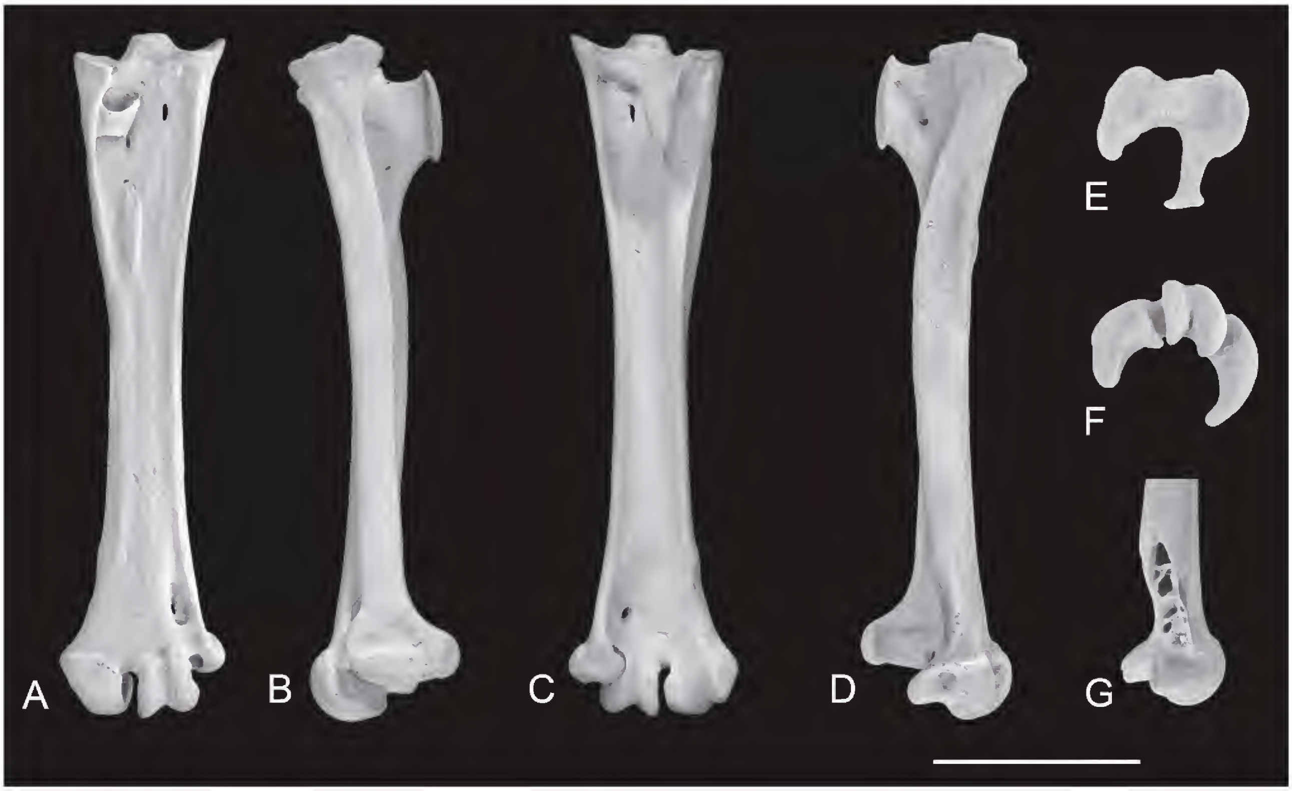


Figure 1. Holotypic tarsometatarsus of *Oraristrix brea* (LACM RLB E9379) in (*A*) anterior, (*B*) lateral, (*C*) posterior, (*D*) medial, (*E*) proximal, and (*F*) distal views. Lateral view (*G*) of distal tarsometatarsus of *O. brea* (LACM RLB K9623) illustrates the straight posterior edge of the lateral condyle of Trochlea III. Scale bar = 20 mm.

Systematics

Order Strigiformes

Family Strigidae

Oraristrix new genus

Type and only included species. *Strix brea* Howard, 1933.

Diagnosis. The tarsometatarsus of *Oraristrix* (Fig. 1) is diagnosed by having (1) Crista medialis hypotarsi with posterior surface long and relatively narrow (posterior surface broad, narrow, or egg-shaped, but moderately long to short in *Strix*; posterior surface either egg-shaped or broad, moderately long to short in *Bubo*); (2) Crista medialis hypotarsi with medial edge of posterior surface concave, in posterior view (posterior surface with variable medial edge in *Strix*; posterior surface rarely with slightly concave medial edge in *Bubo*); (3) Crista medialis hypotarsi extending posteriad and laterad such that posterior lateral edge of hypotarsus lies farther laterally than anterior base (extends less laterad in *Strix*; extends posteriad closer to perpendicular to transverse plane of bone in *Bubo*); (4) Crista medialis hypotarsi with internal side deeply concave (internal side moderately to deeply concave in *Strix* and moderately concave in *Bubo*); (5) Crista medialis hypotarsi bordered medially by prominent angular ridge (a moderate to strongly angular ridge present in *Strix* and only a weak, rounded ridge present in *Bubo*); (6) Cotyla lateralis with posterolateral process, in lateral view, joining posterolateral edge of shaft rather abruptly (process joins posterolateral edge of shaft abruptly to gradually in *Strix*; process joins posterolateral edge of shaft gradually in *Bubo*); (7) Trochlea metatarsi II, in medial view, with "wing" directed posteriad, or plantarad, and with only a slight trend distad (more rounded, in medial view, with posterodistal corner with significant turn distad in *Strix* and *Bubo*); (8) Trochlea metatarsi III, in distal view, with external rim bulging laterad sufficiently to hide distal foramen (similar, but not as extreme, in *Strix*; does not bulge laterad sufficiently to hide distal foramen in *Bubo*); (9) Trochlea metatarsi III with lateral rim straight posteriorly, in lateral view (similar in *Strix*; lateral rim anteroposteriorly rounded and projecting much farther posteriad than medial rim, in lateral view, in *Bubo*); (10) Trochlea metatarsi IV extends farther distad relative to Trochlea metatarsi III than that of *Strix* and much farther distad relative to Trochlea metatarsi III of *Bubo*.

Etymology. *Oraristrix*, from *orarius*, Latin, of the coast, and *strix*, Latin, owl. In reference to the species' known late Pleistocene distribution in coastal southwestern California.

Oraristrix brea (Howard, 1933), new combination

Strix brea Howard, 1933, (March 17), *Condor* 35(2), p. 66, fig. 15 [sic].

Figs 1, 4–6, 8

Types. HOLOTYPE, complete left tarsometatarsus, LACM RLB E9379. PARATYPES: Rancho La Brea: 8 complete right and 9 complete left tarsometatarsi; 1 proximal right and 1 distal left tarsometatarsus.

Referred material. Rancho La Brea: Rostrae maxillare, 2; mandible, 1 anterior with symphysis; sternae, 3; scapulae, 5 right, 9 left; coracoids, 5 complete and 1 scapular end right, 4 complete and 2 scapular ends left; clavicula, 1 right dorsal end; humeri, 3 complete right and 2 complete left, 1 proximal right and 2 proximal left, 1 distal right and 2 distal left; ulnae, 1 complete right, 3 proximal right and 2 proximal left, 2 distal right and 2 distal left; radii, 5 proximal left, 2 distal right and 2 distal left; carpometacarpi, 7 complete right and 4 complete left, 2 distal right; femora, 2 complete right and 3 complete left, 2 proximal left, and 5 distal right and 5 distal left; tibiotarsi, 2 complete right and 3 complete left, 1 proximal right and 5 proximal left, 9 distal right and 3 distal left; fibulae, 3 proximal left; pelves, 2. For catalogue numbers, see Appendix 1.

Carpinteria. Locality LACM(CIT) 139: Rostrum maxillare, 1; coracoids, 1 right and 1 left; humeri, 1 complete left and 1 proximal left; carpometacarpus, 1 incomplete left; tarsometatarsus, 1 complete left. Collections of Santa Barbara Museum of Natural History: Coracoid, sternal end, left; tibiotarsus, distal, right.

Emended diagnosis. As for genus.

Type locality and horizon. Asphalt deposits of Rancho La Brea, at a depth of 3.7–4.9 m (12–16 feet) in Pit 16, Los Angeles, California.

Age. Late Pleistocene.

Description. *Oraristrix brea* was approximately the same size overall as modern *Bubo virginianus* and *Strix nebulosa*, but it was far larger than both *S. varia* and *S. occidentalis*, as noted by Howard (1933). In general, the bones of *O. brea* are more slender, or more lightly built, than those of both *B. virginianus* and *S. nebulosa*, although some elements are more robust in some measurements. *Oraristrix brea* also differs in its limb proportions from those species. Thus, in addition to the diagnostic osteological characters, differences between *Oraristrix, Strix*, and *Bubo* are apparent in both intra- and inter-element and intermembral proportions (see, e.g., Figs 2, 3). For measurements of all elements, see Table 1.

Tarsometatarsus (Figs 1A–G, 2, 3). This bone was discussed in greater detail than any other by Howard (1933), who described five morphological characters and a number of ratios differentiating the extinct species from *Strix occidentalis, S. varia*, and *Bubo virginianus*. Our characters 1, 2, 3, and 9 above are four of these characters that we found to hold up well with our larger comparative series of modern species. However, we found that Howard's (1933:66) distinguishing character 2 ("distal margin of this surface [i.e., posterior, or plantar, surface of internal calcaneal ridge] (as seen in lateral view) sharply defined from portion of calcaneal ridge immediately distal to it, even overhanging") did not consistently distinguish *Oraristrix brea*.

Rostrum maxillare (Fig. 4A–C). Characterized by having (1) Os nasale with posterior edge sloping steeply anteriad, in lateral view [sloping significantly less steeply in *Bubo* (except in *Nyctea* where slope is similar to that of *Oraristrix*) and *Strix*]; (2) Fossae nasales with long axis at steeper angle to Crista tomialis than in either *Bubo* or *Strix*; (3) Fossae nasales with internal floor deeply excavated, nearly parallel to tomial margin (floor of nares similar in *Bubo*; much less excavated in *Strix*); (4) Crista tomialis extends posteriad ventral to, and separated from, Proc. jugalis for a significant distance, ending as pointed projection (similar to shorter in *Bubo*; extends posteriad under Proc. jugalis only slightly, if any, in *Strix*).

Howard's (1933) only criterion for distinguishing the Rostra maxillare of *Oraristrix* from the many partial *Bubo* specimens in the collection (i.e., turbinates more widely

Table 1. Measurements (mm) of skeletal elements of the late Pleistocene *Oraristrix brea* compared with extant species and fossil *Bubo virginianus* from Rancho La Brea (see Figs 10 and 11 for illustrations of measurements). Measurements given in the order: (number of specimens) arithmetic mean ± standard deviation [observed range].

Measurements	*Bubo bubo*	*Bubo virginianus*	*Bubo virginianus* (fossil)	*Oraristrix brea* (fossil)
Premaxilla				
Anterior height (A)	(4) 12.61±0.69 [11.7–13.3]	(20) 11.42±0.63 [10.41–12.53]	(0)	(3) 12.37±0.37 [12.14–12.79]
Anterior width (B)	(4) 12.50±1.25 [11.07–14.05]	(20) 9.46±0.62 [8.15–10.54]	(0)	(3) 10.56±1.29 [9.19–11.76]
Posterior height (C)	(4) 22.53±0.78 [21.64–23.48]	(20) 20.33±1.09 [18.26–21.91]	(2) [20.29–20.44]	(2) [21.61–22.2]
Tomial length (D)	(4) 32.34±2.13 [29.45–34.45]	(20) 28.05±1.28 [26.08–30.79]	(2) [28.41–31.45]	(3) 30.57±0.89 [29.66–31.44]
Tomial width (E)	(4) 28.65±2.01 [26.57–31.05]	(20) 24.09±1.57 [21.76–28.08]	(1) 24.01	(3) 25.22±2.6 [23.4–28.19]
Sternum				
Total length (A)	(4) 81.9±6.08 [73.27–86.77]	(16) 59.46±4.32 [53.26–72.5]	(6) 66.99±1.37 [64.87–68.48]	(1) 59.23
Ventral width (B)	(4) 38.79±2.59 [36.69–42.42]	(17) 29.72±2.31 [27.29–35.8]	(6) 34.25±1.46 [32.75–36.75]	(3) 29.33±3.55 [26.46–33.3]
Coracoid				
Medial length (A)	(3) 63.01±0.35 [62.6–63.22]	(18) 49.03±3.01 [45.23–55.48]	(28) 53.27±1.66 [50.05–57.05]	(10) 47.68±1.65 [44.56–49.32]
Depth of acrocoracoid (B)	(4) 11.75±0.48 [11.06–12.15]	(18) 9.00±0.68 [7.88–10.59]	(28) 9.68±0.46 [8.66–10.42]	(13) 8.85±0.46 [7.95–9.29]
Width of acrocoracoid (C)	(4) 9.87±0.45 [9.32–10.38]	(18) 7.33±0.61 [6.46–8.76]	(28) 8.07±0.46 [7.05–8.96]	(12) 6.48±0.41 [5.48–7]
Width of shaft at procoracoid (D)	(4) 14.53±0.57 [14.17–15.38]	(16) 10.25±0.76 [9.41–12.04]	(28) 11.33±0.52 [10.41–12.46]	(8) 9.31±0.57 [8.22–10.13]
Scapula				
Articular length (A)	(4) 18.71±1.04 [17.59–19.68]	(19) 14.99±1.11 [13.59–18.18]	(43) 16.48±0.84 [14.53–18.09]	(11) 14.06±0.6 [12.75–14.84]
Length of Fac. artic. humeralis (B)	(4) 13.05±0.62 [12.47–13.64]	(19) 9.38±0.74 [8.45–11.27]	(43) 10.5±0.58 [9.36–11.83]	(11) 8.89±0.51 [8.13–9.49]
Width of Fac. artic. humeralis (C)	(4) 8.49±0.47 [8.08–9.16]	(19) 6.42±0.51 [5.64–7.9]	(43) 7.2±0.45 [6.28–8.29]	(11) 6.36±0.4 [5.65–6.81]
Humerus				
Total length (A)	(4) 165.04±10.4 [150.74–174.8]	(18) 124.34±6.15 [113.8–136.82]	(6) 133.59±5.61 [125.37–138.67]	(4) 117.07±3.76 [112.58–121.27]
Proximal width (B)	(4) 29.59±1.9 [26.94–31.14]	(18) 21.09±1.42 [19.05–24.87]	(6) 22.67±1.28 [20.5–23.8]	(5) 20.55±0.68 [19.66–21.24]
Distal width (C)	(4) 27.88±1.56 [25.6–29.08]	(18) 20.32±1.37 [18.49–24.06]	(6) 21.83±1.42 [19.62–23.05]	(6) 19.44±0.57 [18.35–19.91]
Radius				
Total Length (A)	(4) 184.2±11.91 [167–192.3]	(20) 137.21±5.82 [126.62–149.11]	(3) 146.75±7.02 [138.84–152.25]	(0)
Maximum proximal width (B)	(4) 9.69±0.42 [9.16–10.19]	(20) 7.36±0.5 [6.72–9]	(3) 7.97±0.46 [7.46–8.36]	(4) 6.93±0.82 [5.73–7.57]
Minimum proximal width (C)	(4) 6.3±0.57 [5.46–6.69]	(20) 4.55±0.35 [4.02–5.58]	(3) 5.07±0.41 [4.61–5.41]	(5) 4.07±0.11 [3.9–4.22]
Distal width (D)	(4) 13.24±1.32 [11.66–14.88]	(20) 9.78±0.6 [8.77–11.84]	(3) 11±0.58 [10.38–11.53]	(3) 9.64±0.35 [9.37–10.04]
Ulna				
Total Length (A)	(4) 191.1±12.51 [173.1–199.8]	(19) 143.03±6.31 [132.03–157.8]	(6) 154.41±5.48 [147.09–160.5]	(1) 138.25
Proximal width (B)	(4) 17.75±1.08 [16.16–18.57]	(19) 12.95±0.99 [11.57–15.82]	(6) 14.37±0.82 [12.81–15.08]	(1) 13.05
Proximal depth (C)	(4) 14.73±1 [13.28–15.58]	(19) 10.46±0.78 [9.41–12.32]	(6) 11.19±0.54 [10.34–12.05]	(1) 10.42
Width of Condylus dorsalis (D)	(4) 12.3±1.23 [10.69–13.49]	(19) 10.05±0.64 [8.62–11.05]	(6) 11.44±0.38 [11.1–11.94]	(1) 7.67
Carpometacarpus				
Total length (A)	(4) 87.28±5.1 [80.61–92.98]	(18) 64.32±3.13 [57.99–70.26]	(34) 69.14±2.83 [63.45–75.1]	(7) 59.71±1.63 [57.7–62.62]
Proximal width (B)	(4) 18.79±1.06 [17.65–19.98]	(18) 13.74±0.88 [12.39–15.99]	(34) 14.87±0.71 [13.13–16.21]	(7) 13.27±0.38 [12.76–13.78]
Proximal depth (C)	(4) 9.32±0.61 [8.74–9.92]	(18) 7.1±0.47 [6.39–8.4]	(34) 7.73±0.39 [6.76–8.38]	(7) 7.3±0.22 [6.92–7.52]
Depth of mid-shaft (D)	(4) 6.55±0.39 [5.97–6.83]	(18) 4.72±0.37 [3.89–5.39]	(34) 5.09±0.3 [4.35–5.59]	(8) 4.89±0.17 [4.64–5.21]
Distal width (E)	(4) 13.45±0.82 [12.38–14.32]	(18) 10.68±0.73 [9.49–12.46]	(34) 11.82±0.58 [10.62–12.87]	(9) 10.95±0.35 [10.48–11.53]
Pelvis				
Neural arch height (A)	(4) 16.34±1.35 [14.47–17.53]	(19) 11±0.9 [9.86–12.72]	(7) 13.11±0.65 [12.04–14.21]	(2) [10.22–10.39]
Centre height through vertebra (B)	(4) 26.95±2.03 [24.73–29.63]	(19) 18.71±1.2 [17.02–20.68]	(7) 21.47±1.38 [19.19–22.86]	(2) [18.21–18.5]
Width through prezygapop (C)	(4) 13.2±0.88 [12.19–14.33]	(19) 10.06±0.59 [9.12–11.21]	(7) 10.77±0.63 [9.43–11.3]	(2) [10.53–10.76]
Width through antitrochanter (D)	(4) 47.58±1.51 [45.67–49.36]	(19) 37.09±1.9 [34.67–41.86]	(7) 42.48±1.97 [39.13–45.24]	(2) [38.4–38.4]
Width through 1st transverse process (E)	(4) 26.01±1.7 [24.93–28.55]	(19) 20.42±0.92 [18.59–22.02]	(7) 22.48±1.35 [19.5–23.41]	(2) [20.63–22.09]

cont. …

Femur				
Medial length (A)	(4) 94.62±4.25 [89.85–99.89]	(18) 73.97±3.55 [68.85–82.66]	(41) 80.13±2.72 [73.82–85.12]	(5) 75.52±1.31 [73.25–76.6]
Proximal width (B)	(4) 20.53±1.01 [19.45–21.48]	(18) 15±1 [13.32–17.29]	(41) 16.91±0.76 [15.09–18.48]	(6) 14.97±0.34 [14.51–15.4]
Width at mid-shaft (C)	(4) 9.01±0.59 [8.13–9.36]	(18) 6.64±0.48 [5.82–7.74]	(41) 7.42±0.45 [6.45–8.27]	(8) 6.75±0.24 [6.47–7.13]
Depth at mid-shaft (D)	(4) 8.55±0.5 [7.84–8.99]	(18) 6.23±0.52 [5.52–7.52]	(41) 6.94±0.43 [6.09–7.94]	(8) 6.18±0.23 [5.82–6.41]
Distal width (E)	(4) 20.1±1.61 [17.92–21.63]	(18) 15.18±1.16 [13.08–18.15]	(41) 17.1±0.94 [15.23–19.11]	(10) 15.05±0.96 [12.81–16.07]
Distal depth (F)	(4) 17.49±1.79 [15.57–19.86]	(18) 12.47±0.88 [11.23–14.71]	(41) 13.68±0.92 [11.64–15.57]	(9) 12.34±0.53 [11.51–13.02]
Tibiotarsus				
Total length (A)	(4) 146.01±8.43 [134.15–153.48]	(18) 118.57±4.1 [111.78–125.95]	(18) 125.37±5.01 [115.18–133.72]	(5) 117.89±2.91 [112.85–119.92]
Proximal width (B)	(4) 17.78±1.49 [15.71–19.06]	(18) 13.36±0.91 [11.64–15.75]	(18) 14.77±0.79 [13.58–16.04]	(7) 13.3±0.45 [12.58–13.84]
Proximal depth (C)	(4) 19.95±2.5 [17.65–22.75]	(18) 15.01±1.16 [13.04–18.13]	(18) 16.59±1.01 [15.07–18.32]	(6) 15.19±0.5 [14.24–15.52]
Width at mid-shaft (D)	(4) 8.36±0.16 [8.16–8.54]	(18) 6.41±0.41 [5.69–7.35]	(18) 7.27±0.35 [6.61–7.93]	(12) 6.39±0.39 [5.76–6.89]
Distal width (E)	(4) 19.13±1.32 [17.84–20.98]	(18) 14.48±1.17 [12.48–17.36]	(18) 16.16±0.89 [14.6–17.74]	(10) 13.15±0.96 [11.62–14.21]
Cond. lateralis depth (F)	(4) 14.99±1.08 [13.48–15.95]	(18) 11.32±0.8 [9.93–13.32]	(17) 12.25±0.64 [11.45–13.32]	(8) 10.63±0.77 [9.44–11.44]
Cond. medialis depth (G)	(4) 15.95±1.03 [14.4–16.53]	(18) 11.8±0.77 [10.39–13.67]	(18) 12.97±0.71 [11.87–14.1]	(10) 10.82±0.62 [9.72–11.47]
Tarsometatarsus				
Total length (A)	(4) 78.69±3.35 [74.37–81.57]	(20) 61.17±1.88 [57.91–65.43]	(68) 65.3±2.15 [60.43–69.99]	(15) 65.71±1.47 [62.62–68]
Proximal width (B)	(0)	(20) 13.94±1.08 [12.23–16.72]	(68) 15.62±0.89 [13.51–17.4]	(17) 13.44±0.78 [12.39–14.86]
Length of hypotarsus (C)	(4) 10.82±0.68 [10.17–11.42]	(20) 6.84±0.63 [5.62–8.4]	(68) 7.86±0.71 [6.49–9.17]	(16) 8.45±0.6 [7.2–9.13]
Width of hypotarsus (D)	(4) 4.67±0.2 [4.41–4.87]	(20) 3.35±0.3 [2.89–4]	(68) 3.79±0.46 [2.92–4.99]	(14) 2.94±0.46 [2.08–3.63]
Minimum shaft width (E)	(4) 9.45±0.56 [8.78–10.1]	(20) 7.74±0.81 [6.47–9.64]	(68) 8.93±0.69 [7.24–9.93]	(16) 7.14±0.44 [6.33–7.95]
Distal width (F)	(4) 21.66±1.35 [20.00–23.24]	(20) 16.67±1.1 [14.87–19.36]	(68) 18.36±0.99 [16.26–20.12]	(14) 15.83±0.85 [14.48–17.16]

Measurements	***Strix occidentalis***	***Strix varia***	***Strix aluco***	***Strix nebulosa***
Premaxilla				
Anterior height (A)	(7) 9.44±0.44 [8.73–10]	(8) 9.77±0.42 [9.21–10.61]	(8) 7.52±0.44 [6.95–8.34]	(4) 9.98±0.6 [9.47–10.79]
Anterior width (B)	(7) 8.33±0.46 [7.39–8.77]	(8) 8.64±0.71 [7.98–9.97]	(8) 6.04±0.39 [5.45–6.66]	(4) 8.51±0.26 [8.12–8.7]
Posterior height (C)	(8) 16.4±0.43 [15.69–16.93]	(8) 16.67±1.01 [15.26–17.79]	(8) 13.81±0.47 [13.2–14.46]	(4) 19.11±1.52 [16.92–20.34]
Tomial length (D)	(8) 21.51±0.47 [20.85–22.33]	(8) 23.83±1.22 [21.38–25.2]	(8) 19.91±0.59 [18.77–20.5]	(4) 26.78±1.18 [25.7–28.05]
Tomial width (E)	(8) 17.78±0.5 [16.84–18.26]	(8) 19.31±1.09 [18.38–21.4]	(8) 17.41±0.53 [16.48–17.96]	(4) 23.22±1.53 [21.39–25.06]
Sternum				
Total length (A)	(8) 46.91±1.66 [44.2–49.34]	(7) 51.08±2.45 [47.08–54.4]	(8) 41.93±1.81 [39.21–44.54]	(4) 62.06±3.42 [59.12–66.42]
Ventral width (B)	(8) 24.76±0.89 [23.44–25.87]	(7) 25.39±1.71 [22.94–28.24]	(8) 20.67±0.65 [19.82–21.54]	(4) 28.46±1.6 [26.22–29.65]
Coracoid				
Medial length (A)	(8) 40.15±1.36[38.56–42.16]	(9) 41.64±1.67 [38.77–43.59]	(8) 35.09±0.50 [34.22–35.78]	(9) 50.40±1.87 [47.62–52.98]
Depth of acrocoracoid (B)	(8) 7.07±0.30 [6.61–7.51]	(9) 7.83±0.50 [7.05–8.4]	(8) 6.26±0.32 [5.83–6.81]	(9) 9.35±0.48 [8.45–10.22]
Width of acrocoracoid (C)	(8) 5.42±0.24 [5.2–5.83]	(9) 6.03±0.37 [5.43–6.52]	(8) 4.72±0.18 [4.47–4.94]	(9) 7.41±0.68 [6.92–9.16]
Width of shaft at procoracoid (D)	(8) 8.26±0.44 [7.45–8.72]	(9) 8.67±0.67 [7.36–9.6]	(6) 6.75±0.18 [6.46–6.94]	(2) [10.21–10.73]
Scapula				
Articular length (A)	(8) 11.46±0.35 [10.9–11.95]	(9) 12.66±0.56 [11.98–13.61]	(7) 9.33±0.79 [7.83–10.12]	(4) 14.29±2.13 [11.31–16.24]
Length of Fac. artic. humeralis (B)	(8) 7.26±0.25 [6.7–7.48]	(9) 7.5±0.43 [6.9–8]	(7) 6.23±0.33 [5.79–6.7]	(4) 8.98±0.62 [8.46–9.86]
Width of Fac. artic. humeralis (C)	(8) 5.32±0.21 [5.01–5.64]	(9) 5.59±0.45 [4.66–6.18]	(7) 4.85±0.17 [4.59–5.12]	(4) 6.39±0.49 [5.7–6.85]
Humerus				
Total length (A)	(14) 99.7±2.29 [95.84–103.81]	(7) 105.38±2.72 [101.87–108.77]	(19) 86.20±2.26 [81.05–90.95]	(8) 132.58±4.3 [126.32–137.71]
Proximal width (B)	(14) 16.97±0.53 [16.25–17.98]	(7) 18.19±0.81 [17.02–19.31]	(8) 15.23±0.43 [14.37–15.64]	(8) 22.35±0.75 [21.25–23.36]
Distal width (C)	(14) 17.11±0.39 [16.43–17.76]	(7) 17.46±0.92 [16.25–19.18]	(8) 15±0.33 [14.39–15.5]	(8) 22.14±0.94 [20.69–23.26]
continued …				continued …

Table 1 continued. Measurements (mm) of skeletal elements of the late Pleistocene *Oraristrix brea* compared with extant species and fossil *Bubo virginianus* from Rancho La Brea (see Figs 10 and 11 for illustrations of measurements). Measurements given in the order: (number of specimens) arithmetic mean ± standard deviation [observed range].

Measurements	*Strix occidentalis*	*Strix varia*	*Strix aluco*	*Strix nebulosa*
Radius				
Total Length (A)	(8) 104.06±1.87 [101.47–106.97]	(8) 109.35±3.16 [105–113.76]	(8) 89.85±1.27 [87.65–91.9]	(8) 135.79±4.6 [129.53–140.83]
Maximum proximal width (B)	(8) 6.19±0.29 [5.75–6.51]	(8) 5.86±1.38 [3.44–6.99]	(8) 5.46±0.15 [5.3–5.66]	(8) 7.91±0.52 [7.18–8.48]
Minimum proximal width (C)	(8) 3.79±0.12 [3.55–3.91]	(8) 4.59±1.18 [3.61–6.64]	(8) 3.19±0.18 [3.02–3.55]	(8) 4.75±0.28 [4.28–5.01]
Distal width (D)	(8) 8.63±0.36 [8.16–9.27]	(8) 8.56±0.5 [7.75–9.2]	(8) 7.46±0.33 [7.01–7.88]	(8) 10.75±0.41 [9.93–11.23]
Ulna				
Total Length (A)	(11) 108.59±1.99 [106.37–112.64]	(8) 114.87±3.25 [110.43–119.61]	(19) 94.01±2.66 [86.81–99.83]	(8) 142.72±5.08 [135.75–148.46]
Proximal width (B)	(11) 10.58±0.39 [9.97–11.09]	(8) 10.99±0.51 [10.33–11.98]	(8) 9.45±0.26 [9.06–9.78]	(8) 13.65±0.53 [12.92–14.22]
Proximal depth (C)	(11) 8.56±0.37 [7.97–9.05]	(8) 8.97±0.48 [8.39–9.67]	(8) 7.44±0.16 [7.17–7.71]	(8) 11.56±0.38 [10.83–12.05]
Width of Condylus dorsalis (D)	(11) 8.88±0.39 [8.3–9.43]	(8) 9.02±0.58 [8.47–10.21]	(8) 7.62±0.71 [6.52–8.8]	(8) 10.55±0.52 [9.48–11.03]
Carpometacarpus				
Total length (A)	(6) 50.06±1.69 [47.79–51.99]	(8) 53.85±1.9 [50.68–56.96]	(19) 44.74±1.21 [42.51–47.20]	(8) 64.98±3.01 [60.06–68.24]
Proximal width (B)	(6) 11.97±0.38 [11.54–12.59]	(8) 11.86±0.48 [11.22–12.66]	(8) 10±0.27 [9.63–10.34]	(8) 14.81±0.62 [13.61–15.61]
Proximal depth (C)	(6) 6.08±0.36 [5.7–6.68]	(8) 6.42±0.25 [6.08–6.81]	(8) 5.26±0.19 [4.91–5.47]	(8) 7.77±0.36 [7.28–8.37]
Depth of mid-shaft (D)	(6) 3.73±0.17 [3.52–3.91]	(8) 4.04±0.08 [3.89–4.13]	(8) 3.54±0.15 [3.37–3.76]	(8) 5.41±0.24 [5.04–5.66]
Distal width (E)	(6) 9.8±0.36 [9.37–10.29]	(8) 9.81±0.63 [9.12–10.98]	(8) 8.27±0.35 [7.64–8.66]	(8) 11.66±0.61 [10.88–12.58]
Pelvis				
Neural arch height (A)	(12) 8.39±0.73 [7.36–9.28]	(9) 9.68±0.67 [8.92–10.88]	(8) 7.34±0.29 [6.9–7.61]	(4) 12.19±1.24 [10.59–13.63]
Centre height through vertebra (B)	(12) 15.07±0.69 [14.01–16.29]	(9) 16.43±0.85 [15.47–17.57]	(8) 13.05±0.4 [12.21–13.42]	(4) 20.26±1.42 [18.33–21.75]
Width through prezygapop (C)	(12) 7.9±0.17 [7.68–8.23]	(9) 8.02±0.31 [7.6–8.48]	(8) 7.5±0.16 [7.27–7.78]	(4) 10.35±0.99 [9.39–11.63]
Width through antitrochanter (D)	(12) 31.83±1.18 [29.85–33.73]	(8) 33.21±1.94 [30.86–35.2]	(7) 27.93±1 [26.93–29.8]	(4) 38.67±1.79 [36.74–41.06]
Width through 1st transverse process (E)	(12) 15.53±0.61 [14.73–16.52]	(9) 17.43±0.58 [16.72–18.35]	(8) 14.88±0.36 [14.44–15.44]	(4) 21.7±1.89 [19.2–23.54]
Femur				
Medial length (A)	(15) 64.41±1.58 [62.27–67.17]	(8) 70.11±1.48 [67.56–72.2]	(19) 59.05±1.93 [55.45–91.92]	(9) 85.04±2.68 [82.35–90.33]
Proximal width (B)	(15) 11.87±0.36 [11.25–12.32]	(7) 13.42±0.62 [12.83–14.4]	(8) 10.82±0.2 [10.51–11.09]	(9) 15.77±0.72 [14.73–16.77]
Width at mid-shaft (C)	(15) 5.13±0.16 [4.88–5.44]	(8) 5.73±0.32 [5.36–6.28]	(8) 4.5±0.17 [4.22–4.75]	(9) 6.47±0.41 [5.65–6.95]
Depth at mid-shaft (D)	(15) 4.91±0.26 [4.51–5.48]	(8) 5.39±0.34 [4.99–5.83]	(8) 4.59±0.18 [4.36–4.81]	(9) 6.72±0.15 [6.48–6.95]
Distal width (E)	(15) 12.29±0.46 [11.67–13.07]	(8) 13.51±0.82 [12.62–14.92]	(8) 11.21±0.42 [10.73–11.83]	(9) 16.79±0.85 [15.19–17.34]
Distal depth (F)	(15) 9.86±0.31 [9.45–10.42]	(8) 11.4±0.54 [10.75–12.27]	(8) 9.19±0.64 [7.88–9.84]	(9) 14.39±0.76 [12.81–15.25]
Tibiotarsus				
Total length (A)	(8) 96.27±2.05 [93.56–98.74]	(8) 105.62±2.28 [102.23–108.14]	(19) 86.15±2.59 [79.33–91.92]	(8) 118.99±3.85 [114.5–125.8]
Proximal width (B)	(8) 10.97±0.27 [10.53–11.33]	(8) 11.38±0.61 [10.72–12.31]	(8) 9.63±0.43 [9.14–10.34]	(8) 13.78±0.64 [12.91–14.66]
Proximal depth (C)	(8) 12.26±0.52 [11.49–12.96]	(8) 13.16±0.7 [12.54–14.53]	(8) 11.29±0.44 [10.76–11.86]	(8) 16.21±0.62 [15.1–16.94]
Width at mid-shaft (D)	(8) 4.94±0.13 [4.79–5.14]	(8) 5.42±0.3 [4.98–5.98]	(8) 4.5±0.12 [4.29–4.72]	(8) 6.14±0.29 [5.65–6.55]
Distal width (E)	(8) 11.38±0.36 [10.81–11.73]	(8) 11.91±0.79 [11.08–13.17]	(8) 9.77±0.31 [9.33–10.16]	(8) 14.49±0.49 [13.5–14.98]
Cond. lateralis depth (F)	(8) 9.24±0.26 [8.81–9.55]	(8) 9.88±0.39 [9.45–10.48]	(8) 8.07±0.18 [7.72–8.24]	(8) 11.85±0.67 [10.61–12.45]
Cond. medialis depth (G)	(8) 9.45±0.35 [8.87–9.79]	(8) 9.99±0.34 [9.6–10.57]	(8) 8.28±0.27 [7.86–8.67]	(8) 11.73±0.58 [10.85–12.45]
Tarsometatarsus				
Total length (A)	(10) 55.04±1.08 [53.6–56.62]	(8) 57.95±2.46 [53.01–60.35]	(19) 48.62±1.13 [46.33–50.45]	(8) 57.06±2.06 [54.15–59.92]
Proximal width (B)	(10) 11.32±0.55 [10.29–11.88]	(8) 11.84±0.77 [10.99–13.09]	(3) 9.38±0.12 [9.27–9.5]	(7) 14.62±0.37 [13.99–15.2]
Length of hypotarsus (C)	(10) 5.63±0.36 [5.16–6.28]	(8) 7.37±0.57 [6.27–7.93]	(8) 6.19±0.56 [5.46–7.03]	(8) 8.09±0.6 [7.15–9.02]
Width of hypotarsus (D)	(10) 2.65±0.14 [2.32–2.84]	(8) 2.74±0.3 [2.37–3.15]	(8) 2.32±0.14 [2.05–2.47]	(8) 3.6±0.21 [3.28–3.86]
Minimum shaft width (E)	(10) 5.84±0.23 [5.53–6.2]	(8) 6.44±0.53 [5.92–7.26]	(8) 5.11±0.19 [4.97–5.51]	(8) 7.69±0.42 [6.77–8.23]
Distal width (F)	(9) 12.93±0.53 [11.87–13.56]	(8) 14.25±0.83 [13.08–15.57]	(8) 11.23±0.41 [10.71–11.87]	(8) 16.55±0.98 [14.7–17.26]

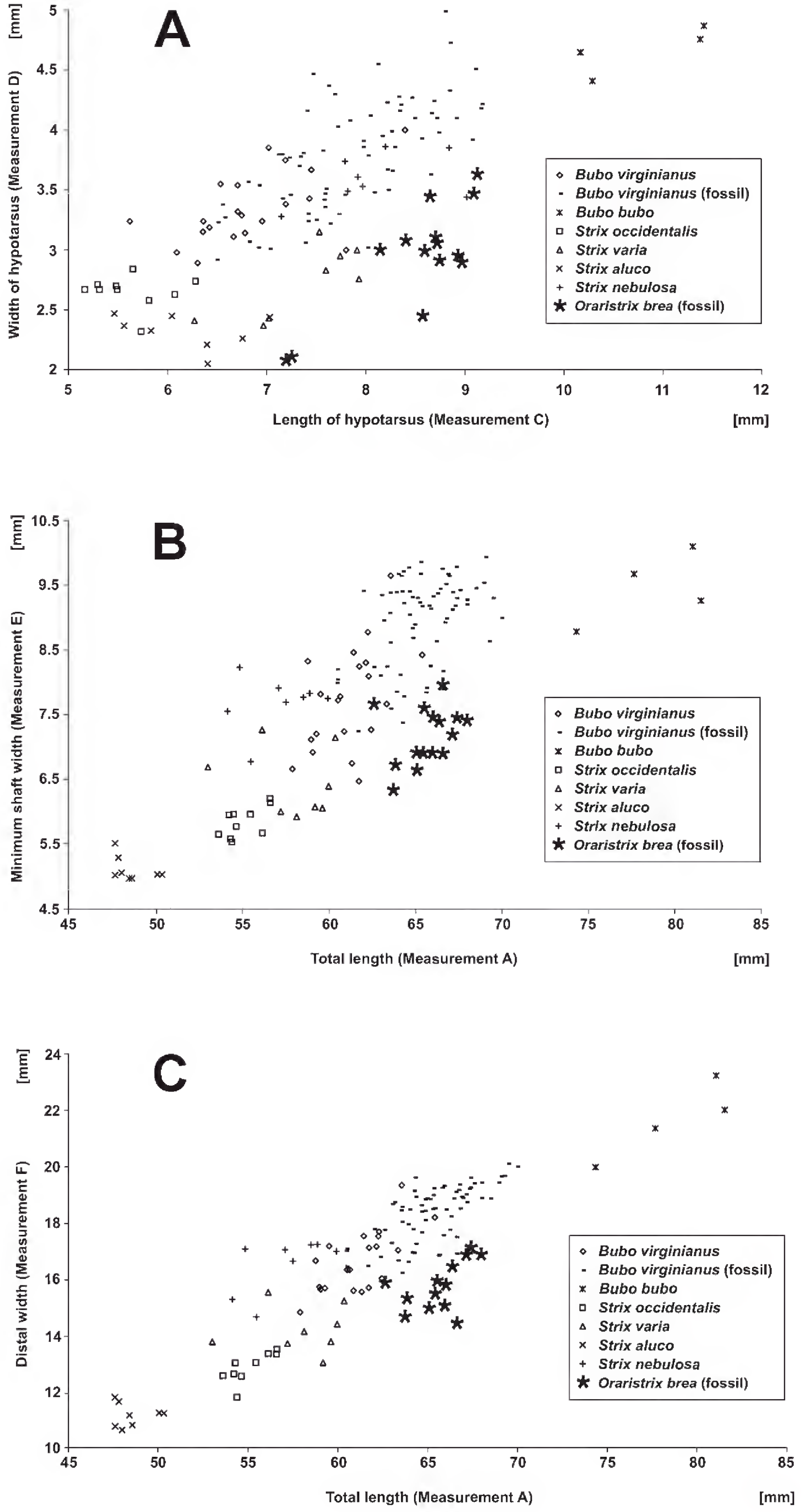


Figure 2. Intra-element proportions of the tarsometatarsus of *Oraristrix brea* distinguish it from modern species of owls. (*A*) Scatter diagram of length *vs.* width of posterior surface of hypotarsus. For its length, the posterior surface of the hypotarsus of *O. brea* is relatively narrow compared to that of modern owls. (*B*) Scatter diagram of total length *vs.* minimum shaft width of tarsometatarsus. The length of *O. brea* is within the upper values for *Bubo virginianus*, but most of the fossils have a relatively slender shaft. (*C*) Scatter diagram of total length *vs.* distal width of tarsometatarsus. The length of *O. brea* is within the upper values for *Bubo virginianus*, but most of the fossils have a relatively narrower distal end.

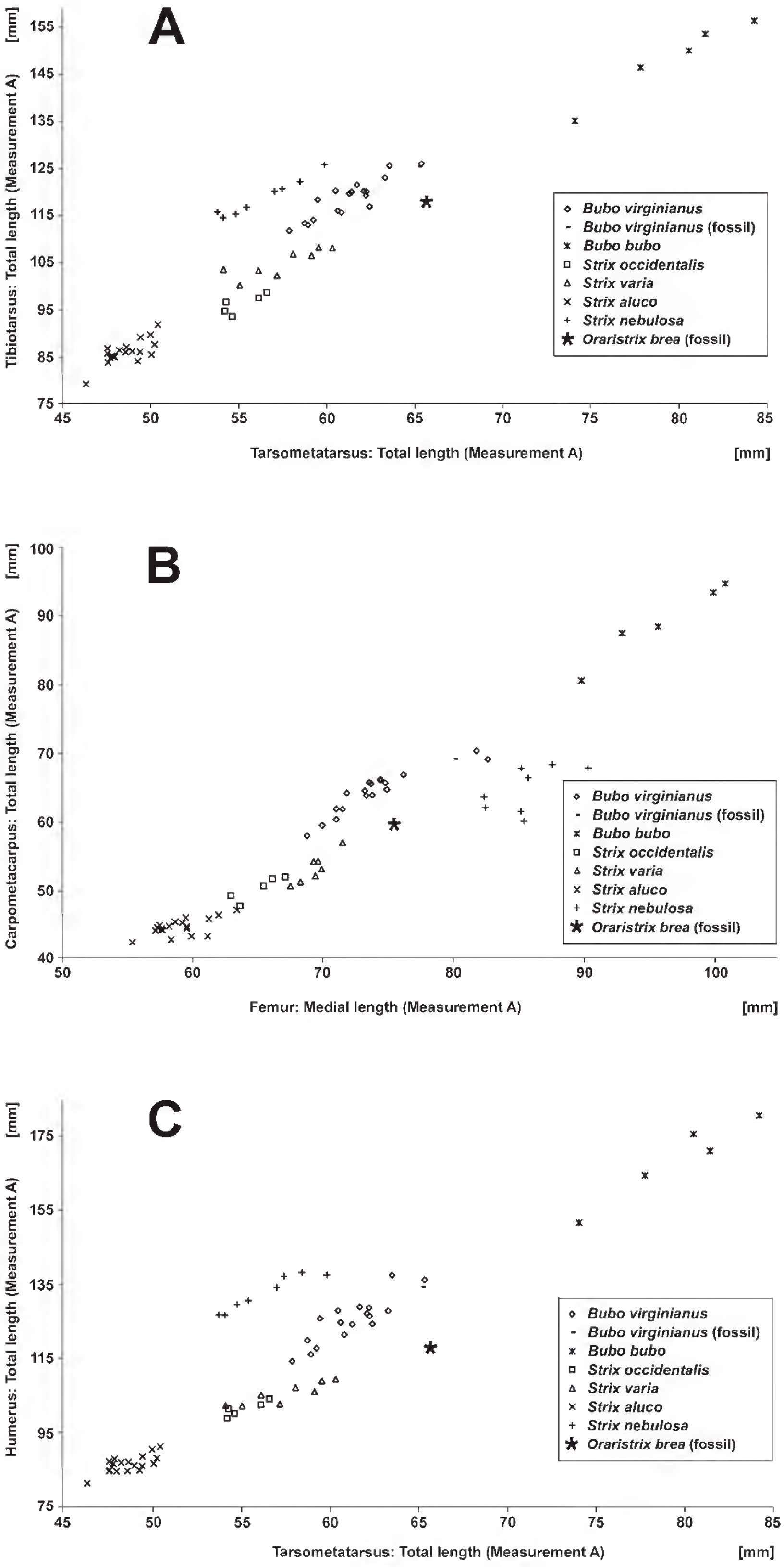
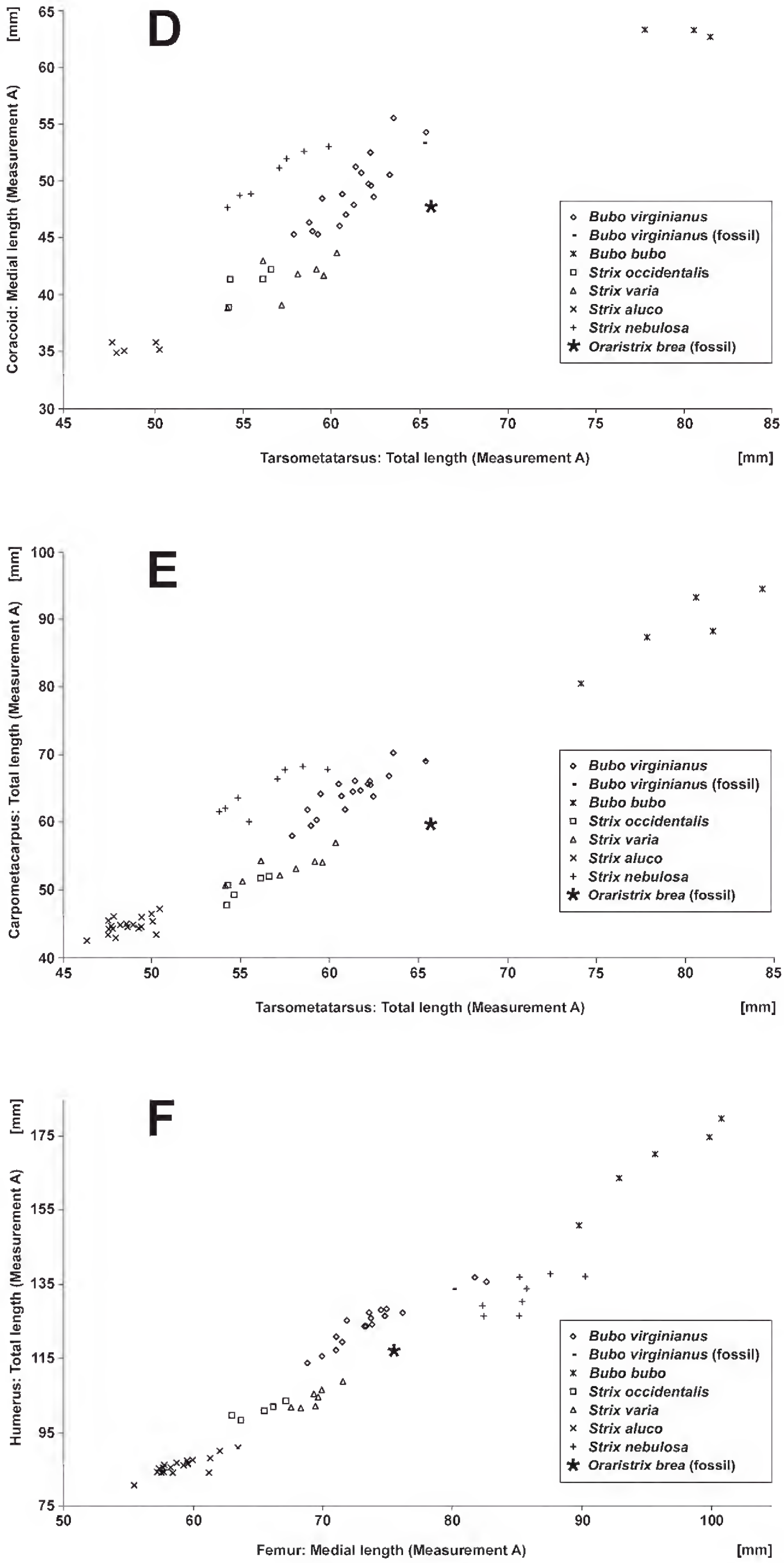


Figure 3. Intra-membral and inter-membral element plots give an indication of how *Oraristrix brea* differed from the modern owls *Bubo bubo, B. virginianus, Strix nebulosa, S. occidentalis, S. varia*, and *S. aluco*. (*A*) Tarsometatarsus length *vs.* tibiotarsus length. (*B*) Femur medial length *vs.* carpometacarpus length. (*C*) Tarsometatarsus length *vs.* humerus length. (*D*) Tarsometatarsus length *vs.* coracoid medial length. (*E*) Tarsometatarsus length vs. Carpometacarpus length. (*F*) Femur medial length vs. humeral length. For the modern species,… [continued on facing page]



[Figure 3. continued from facing page] … each symbol represents one specimen, whereas for *Oraristrix brea* and fossil *Bubo virginianus* from Rancho La Brea the symbol stands for the arithmetic means of all fossil specimens of particular elements. For *O. brea* the number of fossil specimens available for calculating the means was as follows: humerus, 4; coracoid, 10; carpometacarpus, 7; femur, 5; tibiotarsus, 5; tarsometatarsus, 15. For fossil *B. virginianus*, the number of specimens available for calculating the means was as follows: humerus, 6; ulna, 6; carpometacarpus, 34; femur, 41; tibiotarsus, 18; tarsometatarsus, 68.

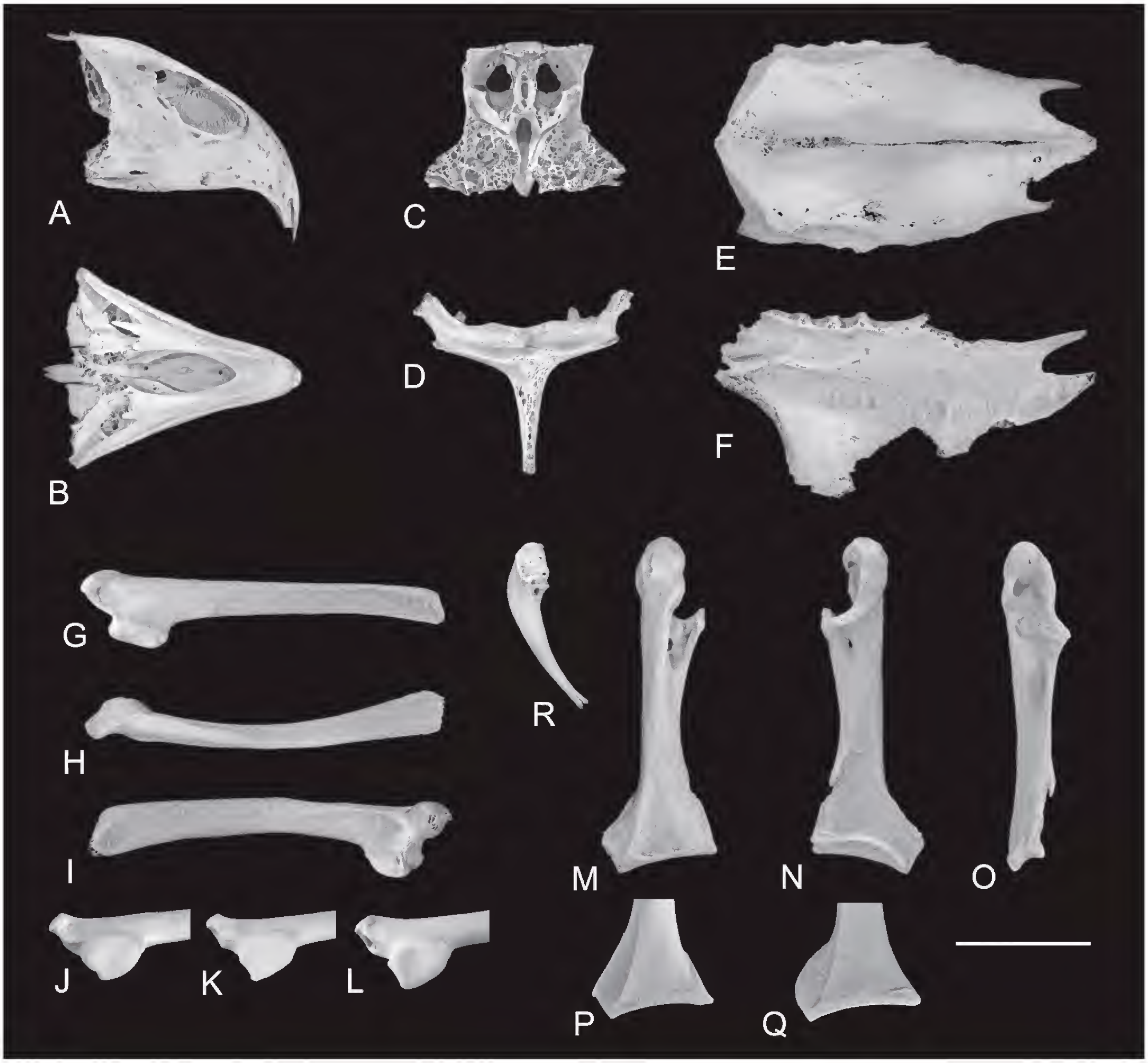


Figure 4. Rostrum maxillare of *Oraristrix brea* (LACM RLB K2713) in (*A*) lateral, (*B*) ventral, and (*C*) posterior views. Sternum of *O. brea* (LACM RLB F2477) in (*D*) anterior, (*E*) ventral, and (*F*) lateral view. Scapula, left, of *O. brea* (LACM RLB H6613), in (*G*) dorsolateral, (*H*) dorsomedial, and (*I*) ventromedial views. Close-up of glenoid facet of (*J*) *O. brea* (LACM RLB H6613), (*K*) *Bubo virginianus* (LACM 109120), and (*L*) *Strix nebulosa* (MVZ 151874) illustrating the consistent differences in the shape of this facet among the species. Coracoid, right, of *O. brea* (LACM RLB F9687), in (*M*) ventral, (*N*) dorsal, and (*O*) medial view. Sternal ends of (*P*) *B. virginianus* (LACM 109120), and (*Q*) *S. nebulosa* (MVZ 155426) illustrate the differences in their Angulus medialis. The differing placement of the Linea intermusculare and the size of the Fac. artic. sternalis can also be noted. Clavicula, left, of *O. brea* (LACM RLB E9233), in (*R*) lateral view. Scale bar = 20 mm.

separated in median line anteriorly, which we interpret as in ventral view through Concavitas maxillare) is valid for separating the Brea Owl from *Bubo virginianus* and allying it with the traditional species of *Strix*. That is, the turbinates are similar, or even less inflated in *Strix* and markedly more inflated in *Bubo*. However, available species of *Ciccaba*, a genus now included in *Strix*, have well inflated anterior turbinates. On the other hand, the anterior turbinates of *Nyctea*, a genus now included in *Bubo*, are not inflated. Although the Rostra maxillare of all large owl specimens in the Rancho La Brea collections are damaged, most of them preserve the anterior parts of the turbinates and some or all of the other characters mentioned above, and they are identifiable as either *Bubo* or *Oraristrix*.

It is interesting to note that the Rostrum maxillare of *Oraristrix brea* was nearly as tall and long as that of the living Eurasian Eagle-owl, *Bubo bubo*, which is much larger than *B. virginianus*, but it was noticeably narrower (Table 1). What this might indicate about its predatory habits is unclear, but it was a strong predator.

Sternum (Fig. 4D–F). Characterized by having (1) Linea intermusculare beginning at Tub. labri externi or posterior to it (similar in *Strix*; Linea intermusculare begins medial and anterior to Tub. labri externi in *Bubo*) (Howard, 1933); (2) Tub. labrum externi not projecting greatly laterad, resulting in only slight to moderate curvature toward midline of Labrum externi and a shallow Sulci artic. coracoideus dorsal to Tub. labrum externi (Tub. labrum externi projecting more laterad, resulting in slight to moderate curvature to Labrum externi in *Strix* and much greater curvature in *Bubo*, and a deep to very

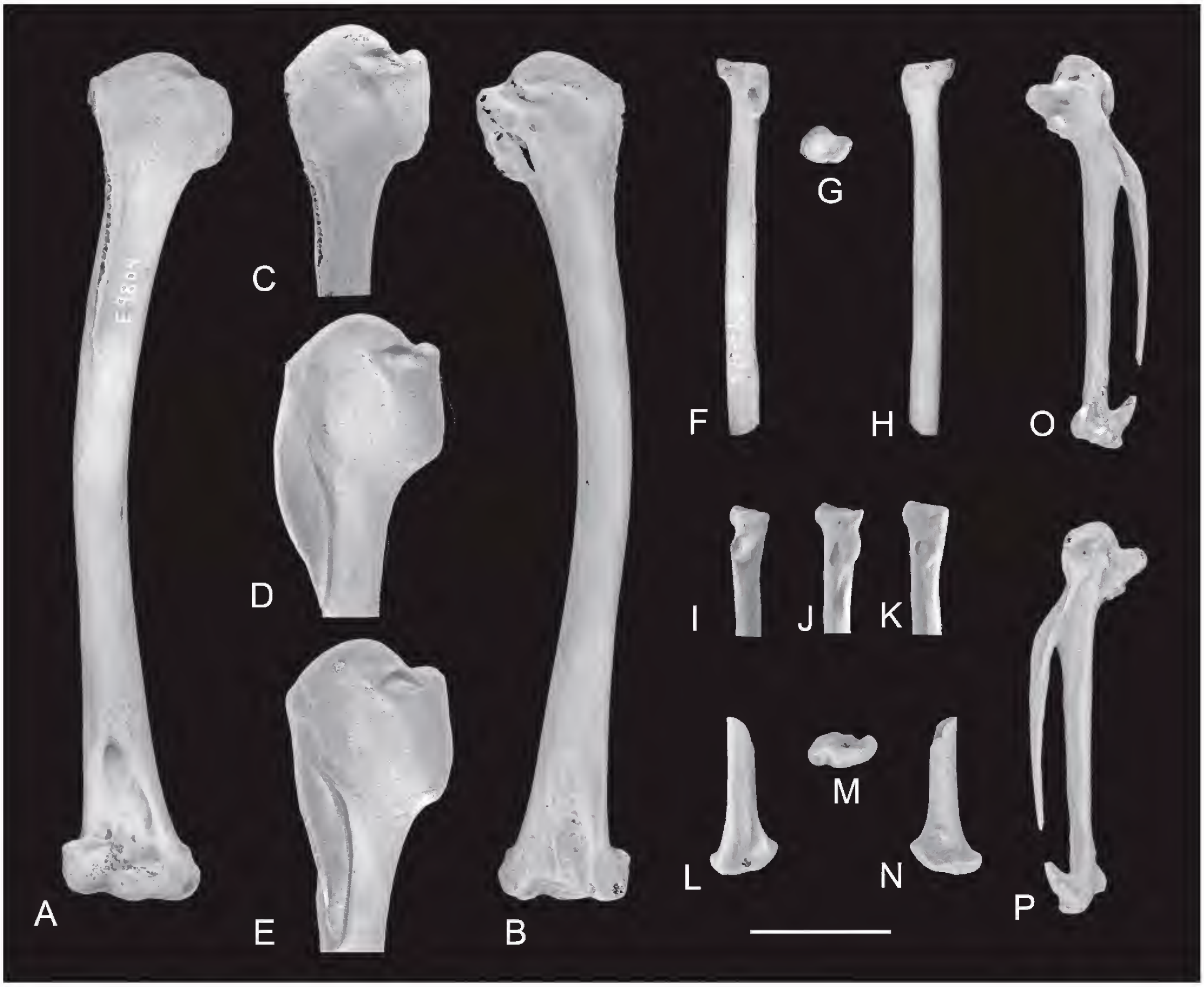


Figure 5. Humerus, right, of *Oraristrix brea* (LACM RLB E9804), in (*A*) anterior and (*B*) posterior view, and (*C*) proximal end in anteroproximal view. Anteroproximal view of proximal ends of (*D*) *Bubo virginianus* (LACM 109226), and (*E*) *Strix nebulosa* (MVZ 155426) illustrates the differences in the form of the Crista bicipitalis and the Sulcus ligamentum transversus. Radius, left, of *O. brea* (LACM RLB K9798), in (*F*) anterior, (*G*) proximal, and (*H*) posterior view. Anteroventral view of left proximal radii of (*I*) *O. brea* (LACM RLB K9798), (*J*) *S. nebulosa* (MVZ 151874), and (*K*) *B. virginianus* (LACM 109226) illustrates the differences in the form and position of the attachment for M. biceps brachii. Radius, distal end, left, of *O. brea* (LACM RLB K9627), in (*L*) dorsal, (*M*) distal, and (*N*) ventral view. Carpometacarpus, left, of *O. brea* (LACM RLB K9432), in (*O*) dorsal and (*P*) ventral view. Scale bar = 20 mm.

deep Sulci artic. coracoideus dorsal to Tub. labrum externi in both *Strix* and *Bubo*); (3) Corpus sternae with Margo posterior pointed, or arrow-shaped, and with Carina sterni extending to tip (Margo posterior of sternum in *Strix* squared off or slightly rounded, moderately wide, with Carina sterni merging before posterior end; Margo posterior of sternum in *Bubo* squared off or centrally notched, moderately wide to wide, with Carina sterni merging before posterior end). The three fossil sternae are too fragmentary to secure many accurate measurements, and minor breakage to Margo posterior of Corpus sternae might have accentuated its pointed form.

Clavicula (Fig. 4R). Characterized by having (1) Fac. artic. acrocoracoidea a moderately deep, elongated oval facing posterolaterad (facet more elongated than oval, less concave, and facing more posteriad in *Strix*; facet more oval, moderately deep, and facing more posteriad in *Bubo*); (2) Fac. artic. procoracoidea small, narrow, not well marked (facet much broader and well marked in *Strix* and *Bubo*); (3) Extremitas omalis claviculae short (long in *Strix* and *Bubo*).

Scapula (Fig. 4G–J). Characterized by having (1) acromion short, blunt-ended, and overall stout (i.e., wider dorsoventrally), in dorsolateral view (acromion much longer, narrower, and slightly less rounded anteriorly in *Bubo*; short to long, narrower, and more pointed anteriorly in *Strix*) (Howard, 1933); (2) Fac. artic. humeralis (glenoid facet) with ventral edge moderately rounded, in medial view (ventral edge nearly straight in *Bubo*; slightly to moderately rounded in *Strix*); (3) Fac. artic. humeralis more rounded than elongated (glenoid facet rounded to elongated in *Strix* and more elongated in *Bubo*); (4) medial surface just posterior to acromion markedly concave with long, prominent, narrow ridge marking dorsomedial corner of bone (area with shallow, elongated depression with long, sharp ridge narrowing posteriad in *Strix*; area with shallow depression and with short to moderately long, prominent ridge narrowing rapidly posteriad in *Bubo*). Characters (2) and (3) were combined by Howard (1933:68) when she referred to the glenoid facet of *Oraristrix brea* as “appearing more ‘heart-shaped’ than *Bubo* …, resembling *Strix* in this character…”.

Coracoid (Fig. 4M–O). Characterized by having (1)

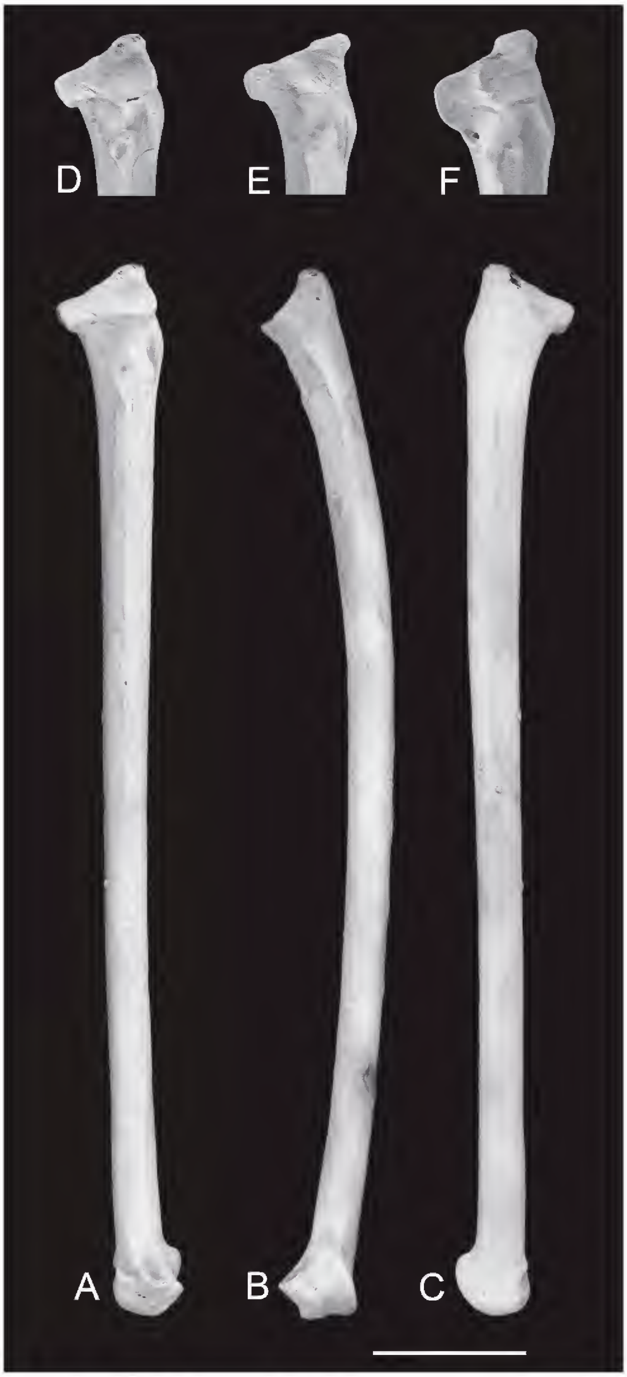


Figure 6. Ulna, right, of *Oraristrix brea* (LACM RLB E9544), in (*A*) anterior, (*B*) ventral, and (*C*) posterior view. Anteroproximal view of (*D*) *O. brea* (LACM RLB E9804), (*E*) *Bubo virginianus* (LACM 87413), and (*F*) *Strix nebulosa* (MVZ 155426) illustrate the differences in form of the olecranon and the position of the Tuberculum lig. coll. ventralis. Scale bar = 20 mm.

Proc. acrocoracoideus claviculae (anterior end, in ventral view) broad, narrowing sharply at Fac. artic. clavicularis [Proc. acrocoracoideus claviculae broad, narrowing slightly via curvature at Fac. artic. clavicularis in *Strix* (excluding *Ciccaba*, where it widens slightly at Fac. artic. clavicularis); Proc. acrocoracoideus claviculae broad, narrowing gradually in *Bubo* (excluding *Nyctea*, where it narrows more abruptly, but less so than in *Oraristrix*) (Howard, 1933); (2) Fac. artic. clavicularis relatively long, narrow, oriented at a slight angle to the long axis of shaft (shorter to long, a relatively narrow oval, oriented at a slightly greater angle to the long axis of shaft in *Strix*; elongated oval to broad oval, not oriented at angle to long axis of shaft in *Bubo*); (3) Proc. procoracoideus with terminus irregularly shaped, with broadened ventral half hosting a small Fac. artic. clavicularis posterior (Fac. artic. clavicularis elongated, blunt, and covering the entire end of a broad, oval Proc. procoracoideus in *Strix* and *Bubo*); (4) shaft ventrolateral to Fac. artic. humeralis gently rounded (shaft more convex in this area in *Strix* and *Bubo*) (Howard, 1933); (5) Fac. artic. sternalis shallow, or narrow, in sternal view, extending mediad beyond tip of Angulus medialis (Fac. artic. sternalis moderately deep to deep in *Strix* and *Bubo*, in sternal view, not extending mediad beyond tip of Angulus medialis); (6) Angulus medialis near 90 degrees, in ventral view (Angulus medialis, in ventral view, moderately to very angular in *Strix* and very angular in *Bubo*); (7) Linea intermusculare ventralis directly in line with Angulus lateralis of Fac. artic. sternalis (similar in *Strix*; Linea intermusculare ventralis positioned medial to Angulus lateralis of Fac. artic. sternalis in *Bubo*).

Howard (1933) described the pneumatization of the Proc. acrocoracoideus claviculae as being less pronounced in *Oraristrix brea* than in *Strix* or *Bubo*. We found this character to be quite variable, even within individuals, and we do not consider it a valid distinguishing character. Character 4 above (from Howard, 1933) is difficult to identify, and it is probably not a readily distinguishing character.

Humerus (Fig. 5A–C). Characterized by having (1) Caput humeri prominently developed ventral to Tub. dorsale (less developed in *Strix* and *Bubo*); (2) Sulcus ligamentum transversus shallow, not extending ventrad past ventral edge of Incisura capitis (extends ventrad as moderately deep groove past ventral edge of Incisura capitis in *Strix*; extends ventrad as a deep groove to well past ventral edge of Incisura capitis in *Bubo*); (3) Crista bicipitalis, in anterior view, short and not extending past ventral edge of Tub. ventrale (long and similar, or extending slightly past ventral edge of Tub. ventrale, in *Strix*; long and extending slightly to well past ventral edge of Tub. ventrale in *Bubo*); (4) Epicondylus dorsalis with prominent spur proximal to proximal end of Condylus dorsalis (similar to very prominent spur at, or just proximal to, proximal end of Condylus dorsalis in *Strix*; very prominent spur, proximal to proximal end of Condylus dorsalis in *Bubo*).

Although Howard (1933) noted a somewhat larger Foramen pneumaticum in *Strix* than in *Bubo*, we found too much variability in this character to consider it reliable. We could not discern the "difficult to describe" differences in form of the attachment of M. brachialis mentioned by Howard (1933:68).

Ulna (Fig. 6A–D). Characterized by having (1) olecranon short, or moderately produced proximad, without proximal end turning ventrad, in anterior view (olecranon short in *Strix*, but with proximal end turning ventrad; olecranon moderate to long in *Bubo*, with proximal end turning ventrad); (2) Tub. lig. coll. ventralis relatively close to rim of Cotyla ventralis (moderate to large distance from rim of Cotyla ventralis in *Strix* and *Bubo*). Howard (1933) did not describe the ulna of *Oraristrix brea*.

Radius (Fig. 5F–I, L–N). Characterized by (1) attachment for M. biceps brachii large, located mostly on posterior side of shaft at a moderate distance from Cotyla humeralis (similar in size, positioned more dorsally, or externally, on

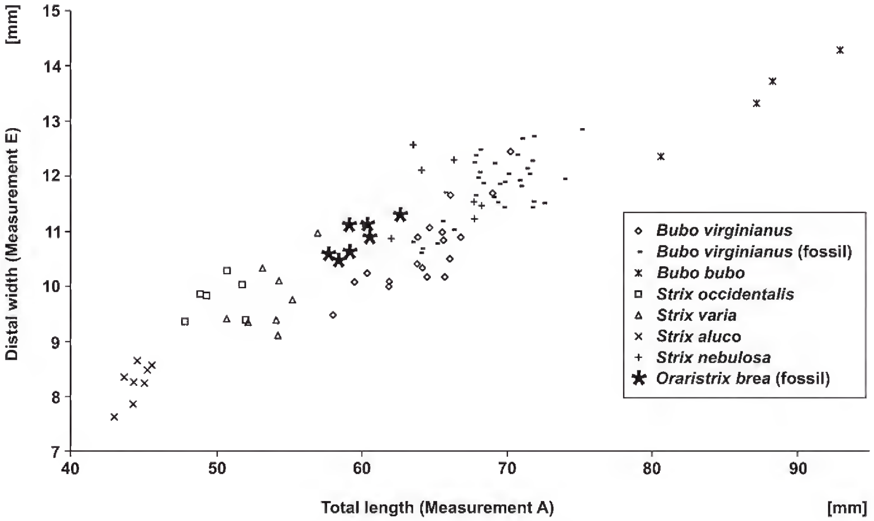


Figure 7. A scatter plot of total length *vs.* distal width of the carpometacarpus of *Oraristrix brea* suggests that this bone had a stout distal end in comparison with that of *Bubo virginianus*, with some overlap with that of *Strix nebulosa*.

shaft and farther from Cotyla humeralis in *Bubo*; attachment area similar in size but with external rim significantly larger, positioned more toward dorsal side of shaft, and at a greater distance from Cotyla humeralis in *Strix*); (2) Cotyla humeralis narrow and elongated (broader and more oval in *Bubo* and *Strix*); (3) distal end with Tub. aponeurosis ventralis short and distinctly set off from edge of shaft, in dorsal view [more elongated and slightly less distinctly set off from edge of shaft in *Strix*; more elongated and not distinctly set off from edge of shaft (i.e., connected to edge of shaft by a long curve) in *Bubo*]. Howard (1933) did not describe the radius of *Oraristrix brea*.

Carpometacarpus (Figs 5O–P, 7). Characterized by having (1) Fac. artic. ulnocarpalis of Trochlea carpalis with ventral portion relatively narrow for length, moderately inflated posterodistally, in posterior view (wider and more inflated posterodistally in *Strix* and *Bubo*); (2) Fac. artic. ulnocarpalis of Trochlea carpalis with posterodistal rim fairly straight, in dorsal view (Fac. artic. ulnocarpalis with posterodistal rim rounded and extending farther posteriad in *Strix* and *Bubo*); (3) Tuberositas metacarpi majoris rounded in anterior view, distinctly set off from shaft proximally (rounded to triangular in *Strix*, less distinctly set off from shaft proximally; triangular shaped in *Bubo*, less distinctly set off from shaft proximally); (4) Os metacarpale minus with a distinct ridge for attachment of M. interosseous ventralis distally (ridge present, but sometimes interrupted in places in *Strix*; ridge absent in *Bubo*) (modified from Howard, 1933); (5) Fac. artic. digitalis minor long, dorsoventrally (relatively slightly longer and more slender in *Strix*; shorter and more robust, or broader, in *Bubo*); (6) area anteroproximal to Fac. artic. digitalis minor (i.e., proximal dorsal symphyseal area between Os metacarpale minus and Os metacarpale majus) flattened, in dorsal view (relatively flattened in *Strix*; narrower and more convex in *Bubo*) (Howard, 1933).

Pelvis (Fig. 8A–C). Characterized by having (1) Os ischium with posterior portion short, tapering rapidly to an angular end (long, tapering gradually to a narrow point in *Bubo* and *Strix*); (2) parapophyses of lumbar and sacral vertebrae robust structures, in ventral view (parapophyses lightly built in *Bubo* and *Strix*).

Femur (Fig. 8F–I). Characterized by having (1) Crista trochanteris merging smoothly with shaft anterodistally, in lateral view (similar in *Strix*; Crista trochanteris merges abruptly with shaft in *Bubo* because its distal end is undercut); (2) attachment of M. iliotrochantericus posterior long, narrow, and located near centre of lateral side of proximal end (attachment shorter, broader, and located near posterior edge of lateral side of bone in *Strix*; longer, narrow, and centrally positioned on side of bone in *Bubo*); (3) Condylus medialis, in posterior view, with lateral end moderately undercut (condyle with lateral end more distinctly undercut, in posterior view, in *Strix* and *Bubo*); (4) Condylus lateralis, in posterior view, as wide as or wider than Trochlea fibularis (similar in *Strix*; condyle narrower than trochlea in *Bubo*); (5) proximal attachment for Impressiones ansae m. iliofibularis (biceps loop) centrally located on lateral side of shaft (centrally to anteriorly located in *Strix*) (Howard, 1933); (6) Crista lateralis of Sulcus intercondylaris immediately anterior to Fovea tendineus m. tibialis anterior not projecting distad to distal edge of, or beyond, Condylus lateralis (similar in *Strix*; projects distad nearly equal to or slightly beyond Condylus lateralis in *Bubo*); (7) Crista lateralis of Trochlea fibularis, in lateral view, well-rounded (Crista lateralis similar to elongated in *Bubo*; less rounded, more elongated posteriad in *Strix*); (8) Condylus lateralis with axis at a significant angle to long axis of shaft (Condylus lateralis nearly parallel with long axis of shaft in *Strix* and *Bubo*); (9) Fovea fibularis broadly and moderately to deeply excavated into lateral side of Condylus lateralis (Fovea fibularis a small, moderate to deep pit not excavated into side of Condylus lateralis in *Bubo* and a moderately deep pit with a portion slightly excavated into side of Condylus lateralis in *Strix*).

Although Howard (1933) correctly noted that in *Bubo virginianus* the proximal attachment for Impressiones ansae m. iliofibularis was located near the anterior edge of the shaft, and was useful for distinguishing *Oraristrix brea* and *B. virginianus*, this character did not hold up well as a generic character when other species of *Bubo* were examined.

Tibiotarsus (Fig. 8L–O). Characterized by having (1) Crista cnemialis anterior extending only slightly proximad of Crista patellaris (similar in *Strix*; extends significantly more

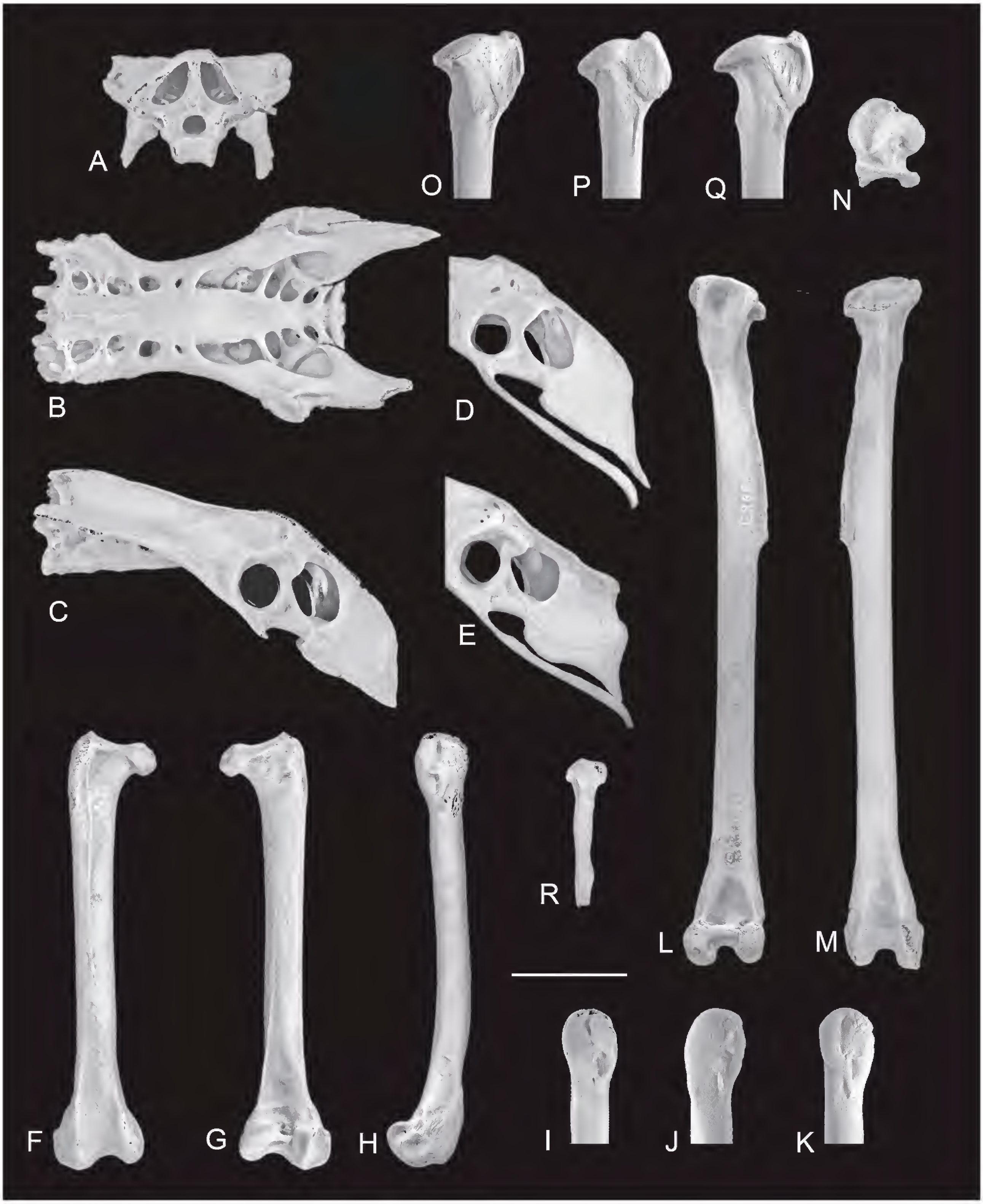


Figure 8. Synsacrum of *Oraristrix brea* (F3700) in (*A*) anterior, (*B*) ventral, and (*C*) lateral view. Views of the posterior ischium of (*D*) *Bubo virginianus* (LACM 110180) and (*E*) *Strix nebulosa* (MVZ 151874) illustrate the differences in the posterior ends of this bone in these species. There is no breakage to the posterior ischium of *O. brea*. Femur, right, of *O. brea* (K9427) in (*F*) anterior, (*G*) posterior, and (*H*) lateral view. Lateral views of the left proximal femur of (*I*) *O. brea* (K9428), (*J*) *S. nebulosa* (MVZ 155426), and (*K*) *B. virginianus* (LACM 109226) illustrate the differences in form of the Crista trochantericus and position of the attachment of M. iliotrochantericus posterior. Tibiotarsus, left, of *O. brea* (E9888) in (*L*) anterior, (*M*) posterior, and (*N*) proximal view. Medial views of left proximal tibiotarsi of (*O*) *O. brea* (E9888), (*P*) *B. virginianus* (LACM 109226), and (*Q*) *S. nebulosa* (MVZ 155426) illustrate the differences in form of the Crista cnemialis anterior and the size and position of the attachment of M. gastrocnemius, pars interna. Fibula, left, of *O. brea* (H9244) in (*R*) lateral view. Scale bar = 20 mm.

proximad in *Bubo*); (2) Fac. artic. medialis with medial and posterior edge well rounded, in proximal view (less rounded and projecting much more posteriad in *Strix* and *Bubo*); (3) Crista cnemialis lateralis long and deeply excavated, or concave, on lateral side (lateral cnemial crest similar in length and excavation in *Strix*; shorter and less excavated in *Bubo*); (4) M. gastrocnemius, pars interna, with distal attachment scar very broad, short, not extending distal to Crista cnemialis anterior (not as broad, longer, extending short distance distal to Crista cnemialis anterior in *Strix*; narrow, very long, extending considerable distance distal to Crista cnemialis anterior in *Bubo*) (Howard, 1933); (5) Fac. artic. lateralis broadened laterally, with relatively low profile (i.e., sloping less steeply laterad), in posterior view (narrower, with much higher profile in *Strix* and *Bubo*); (6) Fac. artic. medialis with flattened anterolateral corner and, in posterior view, no notch between it and Fac. artic. lateralis (facet with anterolateral corner projecting prominently proximad in *Strix* and *Bubo*, with a notch between Fac. artic. medialis and Fac. artic. lateralis); (7) Sulcus extensorius with distal portion (i.e., just proximal to Incisura intercondylaris) deeply and broadly excavated (sulcus generally deep, but slightly less broadly excavated in *Strix*; moderately deep and less broadly excavated in *Bubo*).

Howard (1933:68) stated that she found there was less angular difference present in *Strix* relative to *Bubo* between lines drawn tangent to the proximal and distal edges of the condyles. With additional species and a larger series of comparative material we found this character too variable and difficult to quantify to be reliable for distinguishing genera.

Fibula (Fig. 8R). Characterized by having (1) Caput fibulae without obvious sulcus posterior to lateral tuberosity (sulcus better developed in *Strix* and very well developed in *Bubo*); (2) Caput fibulae deeply excavated anteriorly, with anteromedial corner undercut (deeply, but not as broadly, excavated anteriorly in *Strix*, with anteromedial corner not undercut; robust anteriorly, only slightly concave and not undercut anteriorly in *Bubo*); (3) posterior flange with posteromedial corner rounded, not ending in a pointed protuberance (posteromedial corner ends in a pointed or blunt protuberance in *Strix* and *Bubo*).

Discussion

Comparison with *Grallistrix*. *Grallistrix* Olson & James, 1991, an extinct genus found in the Hawaiian Islands, was interpreted as being derived from *Strix*. *Grallistrix* was diagnosed on the basis of skull characters and the fact that it was a long-legged owl, with a wing length:leg length ratio much different from that of *Strix*. Based on the published illustrations (Olson & James, 1991), *Grallistrix* differs from *Oraristrix* by having a short, broad Crista medialis hypotarsi of the tarsometatarsus, a very angular Angulus medialis of the coracoid, and a more rounded Crista bicipitalis of the humerus that extends ventrad past the ventral edge of the Tub. ventrale, in anterior view. There are undoubtedly many other distinguishing characters, but those listed are the most obvious from the illustrations. The wing length:leg length ratios (humerus + ulna + carpometacarpus : tibiotarsus + tarsometatarsus) of the species of *Grallistrix* are also significantly different than that of *Oraristrix*, being 1.13:1 in *G. orion*; 1.05:1 in *G. geleches*; 1.10:1 in *G. erdmani*, and 1.71:1 in *Oraristrix brea*.

Osteological characters. We identified 138 specimens of *Oraristrix brea* in the Rancho La Brea collections, more than double the 56 specimens identified by Howard (1933). The greater number is a result of additional collections being available and the recognition of additional elements of the skeleton of *O. brea*. The large number of specimens brings out one of the notable attributes of the Rancho La Brea collections, which is that the number of specimens preserved is so great, it is often possible to identify a fairly large number of specimens of extinct species. When all of the major post-cranial bones are available for study it is possible to place osteological characters into a larger context. That is, if a distinctive osteological character is found on one bone, it is sometimes possible to relate it to a distinctive osteological feature on the bone(s) with which it articulates. This ability to trace features from one bone to another was also useful in our study of the extinct California Turkey, *Meleagris californica* (Bocheński & Campbell, 2006).

For *Oraristrix brea*, we noted the following correlations. On the sternum, the Tub. labrum externi does not project very far laterad, which leads to a shallow Sulcus artic. coracoideus. This, in turn, leads to a shallow, or narrow, Fac. artic. sternalis of the coracoid. From this one might infer that the articulation between the coracoid and sternum in *Oraristrix* might have been more flexible than in *Strix* or *Bubo* because the coracoid was not set as deeply into the Sulcus artic. coracoideus as it is in the latter two genera.

The anterior end of the Linea intermuscularis of the sternum begins at the Tub. labrum externi, or posterior to it, in *Oraristrix* and *Strix*, whereas in *Bubo* the anterior portion of the intermuscular line is shifted mediad. The more lateral position of the sternal intermuscular line in *Oraristrix* and *Strix* is reflected in the more lateral position of the Linea intermuscularis ventralis of the coracoid in those genera, which is directly in line with the tip of the Angulus lateralis of the coracoid. In *Bubo*, this intermuscular line lies medial to the Angulus lateralis of the coracoid.

The relatively long and narrow Fac. artic. clavicularis of the coracoid of *Oraristrix*, which is oriented at a slight angle to the long axis of the bone, is reflected in the shape and orientation of the Fac. artic. acrocoracoidea of the clavicula. Also, the lack of a broad, blunt articular facet at the terminus of the Proc. procoracoideus of the coracoid is reflected in the weak, poorly developed Fac. artic. procoracoidea of the clavicula, in contrast to the larger, and presumably stronger, articulation of the procoracoid with the clavicula in *Bubo* and *Strix*.

On the femur of *Oraristrix*, the wide Condylus lateralis is reflected in the broad, relatively low profile of the Fac. artic. lateralis of the tibiotarsus. The size and shape of the Condylus medialis of the femur in *Strix* and *Bubo* is reflected in the more elongated shape, anteroposteriorly, of the Fac. artic. medialis of the tibiotarsus, which is more rounded in *Oraristrix*. The enlarged Fovea fibularis excavated into the lateral side of the Condylus lateralis of *Oraristrix* might result from the lack of a pointed protuberance of the posteroproximal corner of the fibula, as seen in *Strix* and *Bubo*, where the Fovea fibularis is a small to moderately large, deep pit into which the protuberance of the fibula inserts. These character combinations, along with a unique placement of the distal attachment of the M. gastrocnemius, pars interna, the differential between the distal extension of the Condylus lateralis and Condylus medialis, and the greater rounding of the Crista lateralis of the Trochlea fibularis are all suggestive that the knee joint of *Oraristrix* was adapted for a different range of motion, either in locomotion or predation, than *Strix* and *Bubo*.

Size and weight. Howard (1933) observed that the bones of *Oraristrix* were generally more slender than those of *Bubo* and *Strix*. This difference can be observed in scatter diagrams for the tarsometatarsus (Fig. 2). In addition to the bone dimension differences, the differences among the three large owls can now be reasonably estimated by using observed weights of *B. virginianus* and *S. nebulosa* and the calculated weight for *O. brea*. Using the results of a study of the relationship of hindlimb bone dimensions to weight in birds by Campbell & Marcus (1992), the weight of *O. brea* can be calculated using the formula for ordinary least-squares regression: $log(y) = 2.548 \cdot log(x) – 0.414$, where y = mass in grams and x = least shaft circumference of femur in mm. The slope and intercept figures are specifically for the data subset "PB," or predatory birds, of Campbell & Marcus (1992: table 3). The results, when treating the fossil femora of *O. brea* as individuals, have a range of 792–974 g ($x = 868$, $n = 7$). When the fossil femora are treated as a population and the mean of the least shaft circumference of the seven femora is used in the formula $log(\mathrm{y}) = 2.639 \cdot log(x) – 0.517$ (Campbell & Marcus, 1992: table 3), the estimate for the mass of the extinct owl is 900 g. These estimates fall within the low range of observed masses of 680–1450 g (♂) or 1000–2500 g (♀) for *B. virginianus* (Marks *et al.*, 1999) [average masses of various data sets cited in Houston *et al.* (1998) range from 914 to 1318 g (♂) and 1142 to 1769 g (♀)]. Bull & Duncan (1993) cite masses of 825–1050 g ($n = 21$, $x = 890.5$) (♂) and 1025–1700 g ($n = 63$, $x = 1267$) (♀) for *S. nebulosa*. As a test, we used the first equation above and the least shaft circumference of the femora of the comparative specimens of *S. nebulosa* used in this study, which were without recorded mass, to estimate the mass of *S. nebulosa*. The results were 764–1047 g ($x = 970$, $n = 9$). These figures fall within the low part of the mid-range of recorded mass for this species. These results (i.e., mass estimates of *O. brea*), in combination with limb bone measurements, are consistent with the interpretation that *O. brea* was a more slender-bodied bird than *Bubo* or *Strix*.

Howard (1933) also noted that although the length of individual elements of the Brea Owl were closer in size to *Bubo virginianus* than to either *Strix varia* or *S. occidentalis*, in its overall proportions the resemblance was more toward *Strix*. That is, although she found that the leg bones of *Oraristrix brea* tended to be longer than those of *B. virginianus*, the wing elements and coracoid were shorter than the minimum for wing bones of *B. virginianus*. She found a close similarity between *Oraristrix* and *Strix* in ratios of one element to another, except for the coracoid, which seemed to be relatively shorter.

The additional specimens identified for *Oraristrix brea*, including a complete ulna, now allow a more detailed look at wing length versus leg length in this species. Using the mean lengths for the complete limb bones (humerus, ulna, and carpometacarpus for the wing; femur, tibiotarsus, and tarsometatarsus for the leg), we see that the leg of *O. brea* is indeed longer relative to its wingspan than in *Bubo virginianus* and the similar-sized *Strix nebulosa* (Fig. 9A). However, given that femoral length is proportional to body weight (Hertel, 1992; Hertel & Campbell, 2007) and that the femur is held nearly horizontally in birds (Campbell & Marcus, 1992), its length does not necessarily reflect on the height, or stature, of a bird. Including femoral length in the wing length:leg length ratio is comparable to including the coracoid in wing length. That is, femoral length does not affect our visual perception of the stature of a bird. A more accurate representation of the wing length:leg length proportions is gained by using the humerus, ulna, and carpometacarpus for the wing and only the tibiotarsus and tarsometatarsus for the leg (Fig. 9B). This shows a more dramatic difference between the wing length:leg length proportions in *Oraristrix* relative to those of *Strix* and *Bubo*, and it more clearly reveals the long-legged nature of this owl. From this one might conclude that *Oraristrix* was an owl more adapted for ground-dwelling in an open countryside, as opposed to a more "normal" forest owl. This difference in habitat preference might well have led to functional differences that could account for the observed structure of its knee.

Generic status of the Brea Owl. Howard (1933) placed the extinct Brea Owl in the genus *Strix* because she thought that the many osteological characters she identified resembled those of *Strix* more than those of *Bubo*. *Bubo virginianus* is present in large numbers in the Rancho La Brea collections, and initially the specimens of the Brea Owl were even identified as being from that species (Miller, 1916; Husband, 1924; Howard, 1933). The large size of the Brea Owl precluded Howard (1933) from assigning it to either *Strix occidentalis* or *S. varia*, which were the only North American species of owl referred to *Strix* when Howard described the Brea Owl. At that time, the Great Gray Owl, *Strix nebulosa*, was placed in the genus *Scotiaptex*. Although she examined at least one specimen of *S. nebulosa*, she did not comment on any similarities or differences she might have noted between that species and *S. varia* or *S. occidentalis*. She did comment that *Ciccaba*, which she also examined, resembled *Strix* in many characters, and indeed, the species of *Ciccaba* are now placed in *Strix* by some authors, as noted above.

The skeleton of the Brea Owl is an interesting mosaic of many unique osteological characters, and many osteological characters similar to those of *Bubo*, on the one hand, and those of *Strix*, on the other. Although many characters would seem to link *Oraristrix* with *Strix*, as observed by Howard (1933), others appear to link it to *Bubo*. For example, three of the four characters identified for the Rostrum maxillare are more similar to those of *Bubo* than to those of *Strix*, and the fourth is unique. Also, the many interrelated characters of the bones that comprise the knee joint are very suggestive of a mode of locomotion or prey capture in *Oraristrix* that was different from that in *Bubo* or *Strix*. Other characters, such as the narrow Rostrum maxillare, the distinctive shape of the posterior ischium, and the squared-off Angulus medialis of the coracoid, appear to be unique to *Oraristrix* among all owls examined (see list of genera above). Further, in addition to the osteological characters, many intra- and inter-element ratios set *Oraristrix* apart from *Bubo* and *Strix* (e.g., Figs 2, 3). These ratios give us a more complete picture of this owl, in comparison to *Strix* and *Bubo*, but they are informative rather than diagnostic characters. As with all other taxonomic categories, there is no fixed definition as to what comprises a genus, but in this case, we conclude

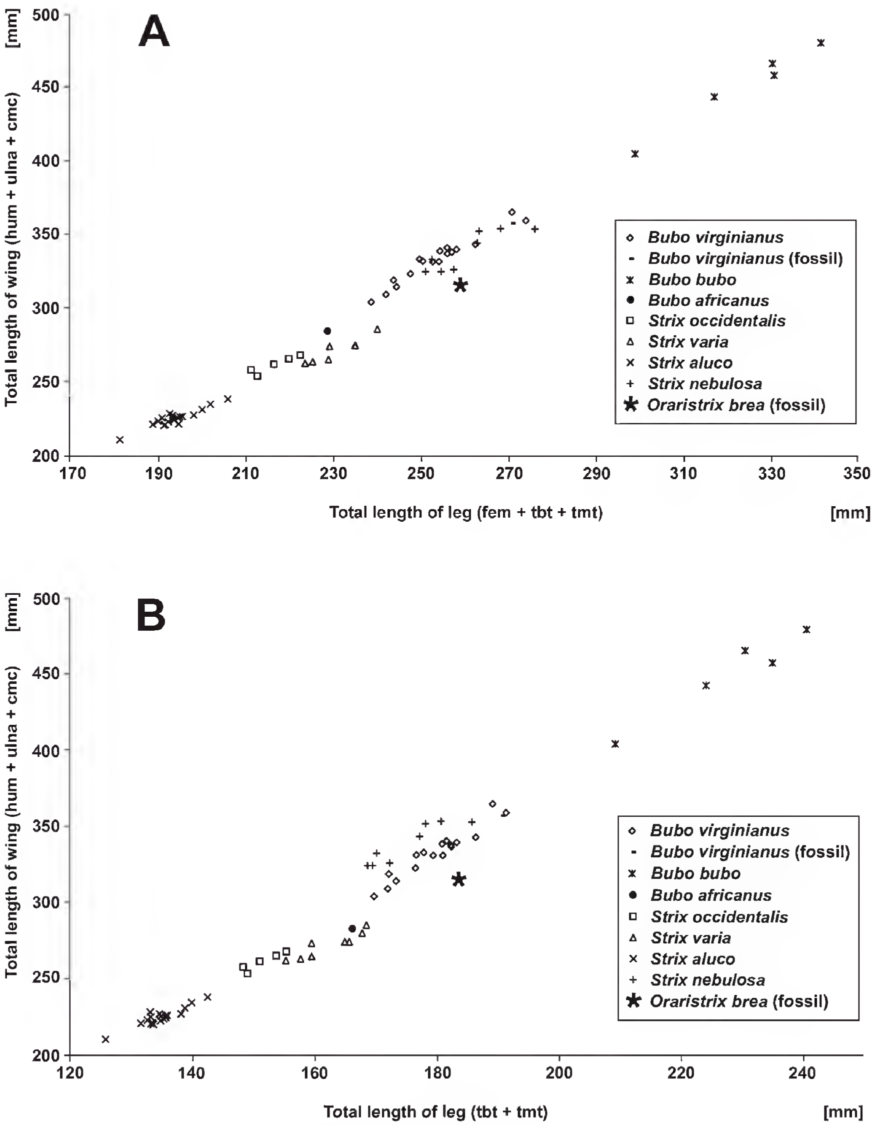


Figure 9. A comparison of wing length *vs.* leg lengths in *Bubo bubo, B. africanus, B. virginianus, Strix nebulosa, S. occidentalis, S. varia, S. aluco*, and *Oraristrix brea*. In (*A*) the leg length includes the femur, whereas in (*B*) only the tibiotarsus and the tarsometatarsus are included in the leg length because the femur is held in a near horizontal position and it correlates with the weight of the bird, not necessarily its stature. In both plots it can be seen that *O. brea* had relatively longer legs in comparison to species of similar wing length. However, the difference might also result from the small number of fossil specimens and/or the fact that the fossil *O. brea* is a composite of an unknown number of individuals. We cannot exclude the possibility, however remote, that the leg elements all, or primarily, belong to large females whereas the wing bones are all from smaller males.
For the modern species, each symbol represents one specimen, whereas for *Oraristrix brea* and the fossil *Bubo virginianus* from Rancho La Brea the symbol stands for the arithmetic means of all fossil specimens of particular elements. For *O. brea* the number of fossil specimens available for calculating the means was as follows: humerus, 4; ulna, 1; carpometacarpus, 7; femur, 5; tibiotarsus, 5; tarsometatarsus, 15. For fossil *B. virginianus*, the number of specimens available for calculating the means was as follows: humerus, 6; ulna, 6; carpometacarpus, 34; femur, 41; tibiotarsus, 18; tarsometatarsus, 68.

that the mosaic of distinctive osteological characters found for the Brea Owl is strong support for the recognition of a new genus.

Given the mosaic of characters, and the lack of complete skeletons (e.g., no skulls are known), it is not possible at the present time to say whether *Oraristrix* is derived from either *Bubo* or *Strix*, or an as yet unknown, extinct lineage. If, as the molecular evidence suggests (Wink & Heidrich, 1999; Wink *et al.*, 2008), *Strix* and *Bubo* are closely related, then the ancestral lineage of *Oraristrix* might remain unresolved for some time.

Distribution at Rancho La Brea. Howard (1962) reported 56 specimens of *Oraristrix brea*, representing a minimum of 17 individuals from seven pits at Rancho La Brea. The 138 specimens we have identified as *O. brea* from Rancho La Brea represent a minimum of 23 individuals from 13 pits (Table 2). Howard (1962) found that the greatest number of specimens of *O. brea* came from Pit 16, which she reported as having almost twice as many individuals of all species of birds preserved as the pit with the second-highest minimum number of individuals of all species of birds at Rancho La Brea. Similarly, we found 58 specimens from Pit 16, almost

Table 2. Distribution of *Oraristrix brea* among the different pits, or excavation sites, at Rancho La Brea, with a summary of minimum number of individuals per pit and in total. Scores given in the form left/right.

	Bliss 29	Pit A	Pit B	3	4	10	16	28	36	61–67	81	Pit 91	LACM 7247	total
Rostrum maxillare	·	·	·	·	1	·	·	·	1	·	·	·	·	2
Mandible	·	1/–	·	·	·	·	·	·	·	·	·	·	·	1
Sternum	·	·	·	1	·	·	2	·	·	·	·	·	·	3
Scapula	·	2/–	·	1/–	·	·	5/4	·	·	·	–/1	1/–	·	14
Furculum	·	·	·	1/–	·	·	·	·	·	·	·	·	·	1
Coracoid	·	·	·	1/–	·	·	2/5	·	·	1/–	·	·	·	9
Coracoid–Scapular end	–/1	2/–	·	·	·	·	·	·	·	·	·	·	·	3
Humerus	·	·	·	1/–	–/1	1/1	–/1	·	·	·	·	·	·	5
Humerus–Proximal	·	1/–	–/1	·	·	·	1/–	·	·	·	·	·	·	3
Humerus–Distal	·	·	·	1/1	·	·	1/–	·	·	·	·	·	·	3
Ulna	·	·	·	·	·	·	–/1	·	·	·	·	·	·	1
Ulna–Proximal	·	·	·	1/–	1/–	·	–/2	·	·	·	·	·	·	4
Ulna–Distal	·	1/1	·	·	·	·	–/1	–/1	·	·	·	·	·	4
Radius														
Radius–Proximal	·	2/–	·	1/–	·	·	1/–	·	·	·	·	·	1/–	5
Radius–Distal	·	1/1	·	·	·	·	1/–	·	·	·	·	·	·	3
Carpometacarpus	1/–	1/–	·	–/1	–/1	·	3/4	·	·	·	·	·	·	11
Carpometacarpus–Distal	·	2/–	·	·	·	·	·	·	·	·	·	·	·	2
Pelvis–Synsacra	·	·	·	·	1	·	1	·	·	·	·	·	·	2
Femur	·	–/1	·	·	1/–	·	2/1	·	·	·	·	·	·	5
Femur–Proximal	·	1/–	1/–	·	·	·	·	·	·	·	·	·	·	2
Femur–Distal	·	2/1	2/–	·	·	·	–/4	·	·	·	·	1/–	·	10
Tibiotarsus	·	·	·	1/–	1/1	·	1/–	·	·	–/1	·	·	·	5
Tibiotarsus–Proximal	·	–/1	1/–	·	1/–	·	3/–	·	·	·	·	·	·	6
Tibiotarsus–Distal	–/2	1/1	–/2	·	–/2	·	–/3	·	·	·	·	·	1/–	12
Fibula	·	1/–	·	·	·	·	1/–	·	1/–	·	·	·	·	3
Tarsometatarsus	1/–	3/3	·	·	2/–	·	4/4	·	·	·	·	·	·	17
Tarsometatarsus–Prox	·	·	·	·	·	·	·	·	·	·	·	·	–/1	1
Tarsometatarsus–Distal	·	1/–	·	·	·	·	·	·	·	·	·	·	·	1
total specimens	5	31	7	11	13	2	58	1	2	1	1	2	3	138
minimum individuals	2	3	2	1	2	1	5	1	1	1	1	1	1	23

twice as many as from Pit A, which produced 31 specimens. Six pits produced only one or two specimens. The presence of *O. brea* in the collections from Carpinteria, California, a coastal site approximately 130 km northwest of Rancho La Brea, suggests that *O. brea* was widespread in the coastal lowlands of southern California in the late Pleistocene.

Other records of *Oraristrix brea*. *Oraristrix brea*, as *Strix brea*, has been reported from four other localities outside of southwestern California. One tentative record was reported from Dry Cave, New Mexico (Hurley, 1972), but this record was later corrected because the specimen represents *Bubo virginianus* (A. Harris, pers. comm., see http://www.utep.edu/leb/pleistNM/). A second record, from Sangamon interglacial deposits at Rancho la Brisca, Sonora, Mexico, was reported by Van Devender *et al*. (1985). Examination of a cast of this specimen, a partial tarsometatarsus, housed at the University of Arizona Laboratory of Paleontology (UALP 10157), revealed that it was more similar to *Strix* than to *Bubo* in having a much shorter, proximodistally, Trochlea metatarsi III, which also had its lateral rim much shorter anteroposteriorly and relatively straight, not rounded, posteriorly. Although the available cast showed that the specimen was strongly abraded in some areas, it differed from *Oraristrix* in having (*a*) Trochlea metatarsi III not bulging laterad, in distal view; (*b*) Trochlea metatarsi III shorter, proximodistally, with long axis at a greater angle to long axis of shaft; (*c*) Trochlea metatarsi IV, in lateral view, more rounded distally; (*d*) Fac. lateralis where leading to Trochlea metatarsi IV much broader anteroposteriorly, in lateral view; (*e*) Fac. medialis flatter and broader anteroposteriorly at mid-shaft; and, although only partially visible, (*f*) Sulcus extensorius clearly not as deep along medial edge of Tuberositas m. tibialis anticus, and groove lateral to Tuberositas m. tibialis anticus more constrained, or narrower. Based on the above characters it must be concluded that the specimen does not represent the Brea Owl. Given the poor condition of the specimen, its true identity remains unknown.

A complete tarsometatarsus (Mesa Southwest Museum P6437) from the late Blancan 111 Ranch local fauna near Safford, southeastern Arizona has been referred to *Oraristrix brea* (D. Steadman, pers. comm.). Also, two additional specimens, a partial tarsometatarsus and an unidentified partial pedal phalanx from upper Pleistocene (Rancholabrean Land Mammal Age) fossil deposits at Térapa in east-central Sonora, Mexico, have been referred to *Oraristrix brea* (D. Steadman, pers. comm.). We were unable to examine these specimens, so we cannot comment on the accuracy of their identifications.

***Oraristrix*: an "island" owl?** In many ways, southwestern, coastal California currently comprises an island. It is bordered on the west by the Pacific Ocean and surrounded to the north, east, and south by high mountains and/or extreme deserts. For sedentary, or non-migratory, species of birds that somehow found their way into southwestern, coastal California there would probably have been little opportunity for interbreeding with ancestral lineages. Isolation would have led to allopatric speciation, although we cannot yet suggest a time of divergence for *Oraristrix* from its ancestral lineage. However, the many osteological differences between *Oraristrix*, on the one hand, and *Bubo* and *Strix* on the other, suggest to us that the time of divergence of *Oraristrix* was well before the late Pleistocene. If the record from the 111 Ranch local fauna is accurate, the species' ancestral lineage might have entered southern California in the latest Pliocene or earliest Pleistocene.

The island analogy is perhaps supported by the allomorphic direction *Oraristrix* took relative to *Strix* and *Bubo*. Specifically, the increase in leg length, and especially of the length of the tarsometatarsus, relative to wing length and the very large premaxillary can be interpreted as features derived from an island lifestyle. As Louchart (2005:170) noted, in island owls "Trends for longer hindlimbs and shorter wings are observed, and are the same as those known in island birds in general. The most general explanations lie in terrestriality, special diets, and sedentarity." This observation follows that of Grant (1965a:364) in which "In North America and Mexico there is a strong tendency for island birds to have a longer tarsus and bill than their mainland counterparts; …" and "The bill is longer because it deals with a greater range of food-sizes, and the tarsus is longer because a greater variety of perches is used." Additional thoughts bearing on this subject are found in Grant (1965b, 1966). Although the wing:leg ratio in *Oraristrix* did not change as dramatically as that seen in the Hawaiian *Grallistrix*, it is still distinctly different from that seen in North American *Strix* and *Bubo*.

In addition to the species of *Grallistrix*, another example of congeneric island owls having lengthened hindlimbs and shortened wings is that of the genus *Mascarenotus* Mourer-Chauviré, Bour, Moutou, & Ribes, 1994 of the Mascarene Islands. Other island owl taxa were reviewed by Louchart (2005).

A final corollary with island owls is the timing of their extinction. As noted by Louchart (2005:170), "For the Strigiformes, even if the exact causes [of extinction] are often very difficult to establish, it was demonstrated in almost all the individual cases that they [reasons for extinction] were anthropogenetic." Although a clear link between the arrival of humans in southern California and the extinction of *Oraristrix brea* cannot be drawn, as opposed to the more obvious possible link noted for the extinction of the California Turkey, *Meleagris californica* (Bocheński & Campbell, 2006), the two events did seem to occur at approximately the same time.

Conclusion

A review of the large, extinct owl from Rancho La Brea has more than doubled the number of specimens and added new skeletal elements to those previously known for that species. A larger series of modern comparative material than that available in 1933, when the species was first described, as well as many more specimens of the extinct species, facilitated the identification and description of more osteological features of *Oraristrix brea*. In some instances, osteological characters could be correlated between articulating bones, thereby placing them into a larger context. The many distinctive characters of the bones comprising the knee joint, for example, suggest that pedal locomotion and/or prey capture was probably different in *Oraristrix* when compared to that of *Strix* and *Bubo*. The estimated weight of *O. brea* is consistent with the interpretation that it was a slender-bodied bird, and its longer legs relative to its wingspan when compared with *Bubo* or *Strix*, as well as many inter- and intra-membranal ratios, set the extinct Brea Owl apart as a long-legged owl. We interpret these features as suggesting that this owl was more terrestrial in habits, favoring coastal scrub habitats, as opposed to being a forest owl. We conclude that the distinctive osteological features of this owl warrant its placement in a new genus, *Oraristrix*.

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Appendix 1

List of catalogue numbers of specimens of *Oraristrix brea* (* indicates photograph of specimen appears in a figure; **H* indicates holotype).

Rancho La Brea

All catalogue numbers of Rancho La Brea specimens carry the prefix "LACM RLB."

Rostrum maxillare			C7125, K2713*
Mandible			K9915
Sternum			F2477*, F2530, D9615
Scapula			
	Right		H6610, H6629, H6659, H6660, H6673
	Left		E2720, H6039, H6065, H6613*, H6636, H6656, K9439, K9440, R11681
Coracoid			
	Right		E9687*, H4850, H4889, H4904, H4911
		Scapular end	K9435
	Left		E9273, H4872, H4881, H4923
		Scapular end	K9436, K9437
Clavicula			E9233*
Humerus			
	Right		E9425, E9804*, F9702
		Proximal	K5261
		Distal	E8911
	Left		F9701, E9051
		Proximal	F9305, K9438
		Distal	G2129, F9538
Ulna			
	Right		E9544*
		Proximal	F1293, G8424
		Distal	G8426, K9750
	Left		
		Proximal	D296, E3170
		Distal	G8435, K9753
Radius			
	Right		
		Distal	K9629
	Left		
		Proximal	E9025, H8036, K9797, K9798*, L481
		Distal	H8026, K9627*
Carpometacarpus			
	Left		E1155, H3107, H3126, K9432*
	Right		E3820, E4504, H3096, H3097, H3098, H3124, K9434
		Distal	K9431, K9433
Pelvis			F1325, F3700
Femur			
	Right		E9647, K9427*
		Distal	F4880, F4883, F4884, F6043, K9424
	Left		B9889, E9439, E9909
		Proximal	K9370, K9428*
		Distal	K9425, K9426, K9429, K9430, R45378
Tibiotarsus			
	Right		E9758, E9932
		Proximal	K9505
		Distal	E1139, E9363, E9919, E9942, F7456, K5259, K9506, K9512, K9513
	Left		E9267, E9414, E9888*
		Proximal	E680, E4347, E9545, E9606, K5260
		Distal	K9503, K9511, R49134
Fibula			
	Left		K1040, H9244*, L483
Tarsometatarsus			
	Right		E9416, E9575, G3933, G3958, K9620, K9621, K9622, K9623*
		Proximal	L482
	Left		E9379*H, E9417, E9892, E9911, G3931, G3957, K9616, K9617, K9619
		Distal	K9618

Carpinteria Locality LACM(CIT) 139

Rostrum maxillare			LACM 154059
Coracoid			
	Right		LACM 154054
	Left		LACM 154055
Humerus			
	Left		LACM 154058
		Proximal	LACM 154060
Carpometacarpus			
	Left		LACM 154056
Tarsometatarsus			
	Left		LACM 154051

Santa Barbara Museum of Natural History

Coracoid		
	Right, sternal end	SBMNH 1243
Tibiotarsus		
	Right, distal	SBMNH 773

Appendix 2

Illustrations of measurements taken (Figs 10–11).

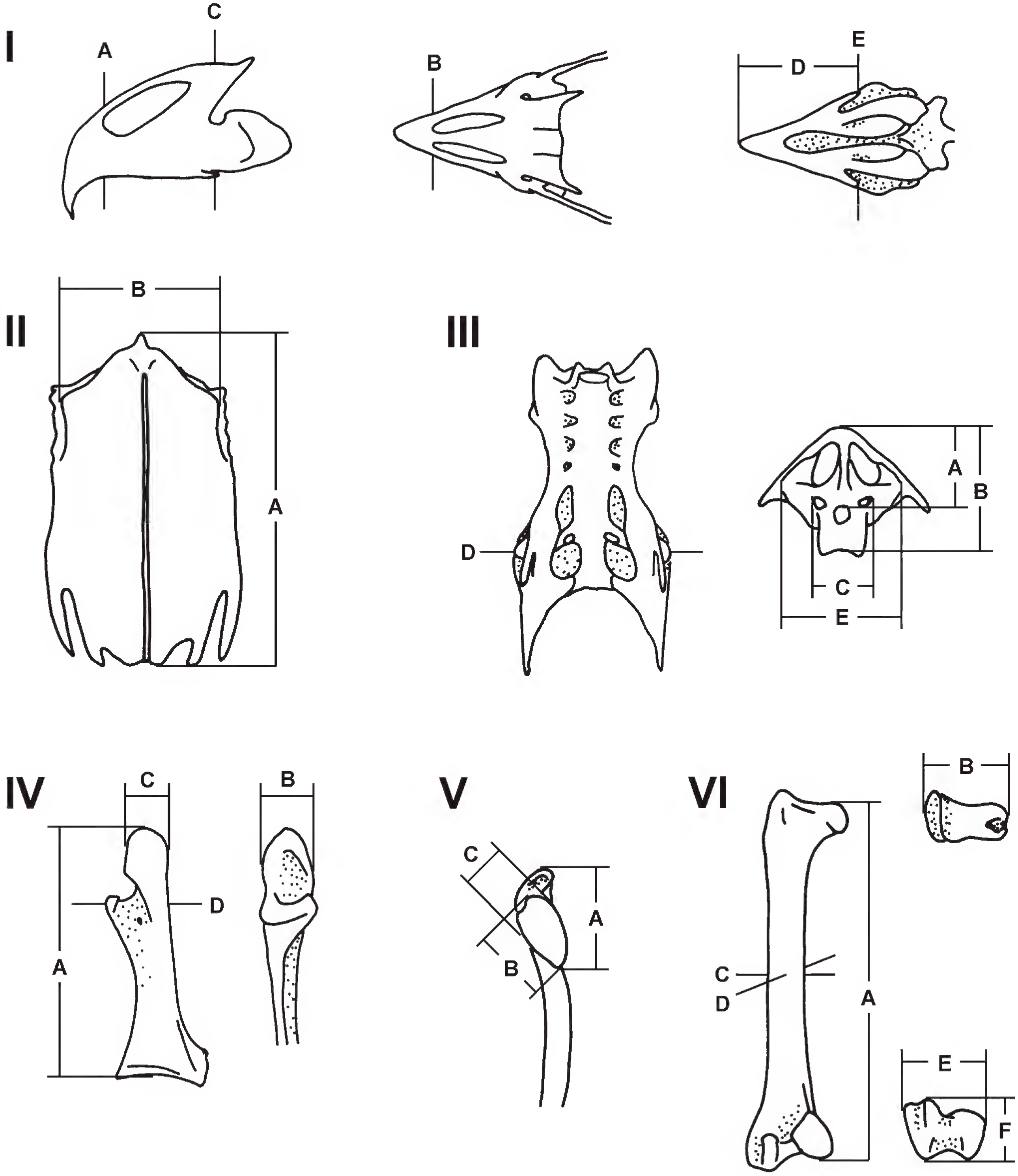

Figure 10. Measurements (refer to Table 1). (*I*) Premaxilla: A, anterior height; B, anterior width; C, posterior height; D, tomial length; E, tomial width. (*II*) Sternum: A, total length; B, ventral width. (*III*) Pelvis: A, neural arch height; B, centre height through vertebra; C, width through prezygapophyses; D, width through antitrochanter; E, width through 1st transverse process. (*IV*) Coracoid: A, length to mid-Fac. artic. sternalis; B, depth of acrocoracoid; C, width of acrocoracoid; D, width of shaft at procoracoid. (*V*) Scapula: A, articular length; B, length of Fac. artic. humeralis; C, width of Fac. artic. humeralis. (*VI*) Femur: A, median length; B, proximal width; C, width at midshaft; D, depth at midshaft; E, distal width; F, distal depth.

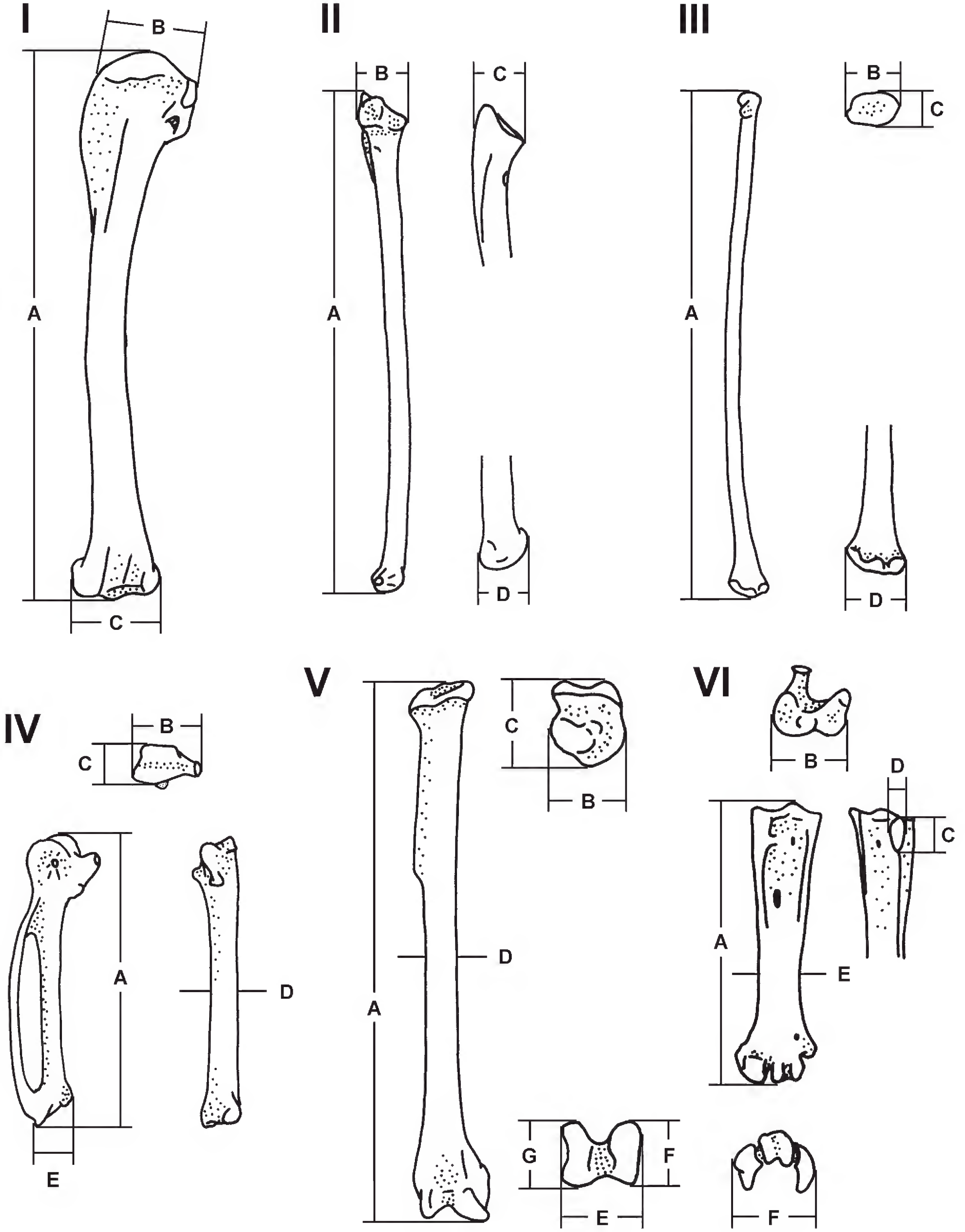

Figure 11. Measurements (refer to Table 1). (*I*) Humerus: A, total length; B, proximal width; C, distal width. (*II*) Ulna: A, total length; B, proximal width; C, proximal depth; D, width of Condylus dorsalis. (*III*) Radius: A, total length; B, maximum proximal width; C, minimum proximal width; D, distal width. (*IV*) Carpometacarpus: A, total length; B, proximal width; C, proximal depth; D, depth of mid shaft; E, distal width. (*V*) Tibiotarsus: A, total length; B, proximal width; C, proximal depth; D, width at midshaft; E, distal width; F, depth of Condylus lateralis; G, depth of Condylus medialis. (*VI*) Tarsometatarsus: A, total length; B, proximal width; C, length of hypotarsus; D, width of hypotarsus; E, minimum shaft width; F, distal width.

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A Revision of C. W. De Vis' Fossil Cormorants (Aves: Phalacrocoracidae)

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ABSTRACT. C.W. De Vis named two species of fossil cormorant, *Phalacrocorax gregorii* and *P. vetustus*, from Pleistocene deposits at Cooper Creek and Warburton River, Australia, based on specimens mainly collected by J.W. Gregory in 1901–1902. The material of each nominal species consists of extensive, syntypic series of mixed elements. It was subsequently regarded that each series comprised specimens from several living species. One of these species, *P. fuscescens*, is an exclusively marine species, raising questions about its purported presence in central Australian deposits. Re-examination of the fossil material confirms that all specimens complete enough for identification can be referred to either of two living species, *P. carbo* or *P. varius*, or occasionally the Darter *Anhinga novaehollandiae*. There is no unequivocal evidence of the occurrence of *P. fuscescens*. Selections of lectotypes are made to synonymize *P. gregorii* with *P. carbo* and *P. vetustus* with *P. varius*.

BOLES, WALTER E., 2010. A revision of C. W. De Vis' fossil cormorants (Aves: Phalacrocoracidae). In *Proceedings of the VII International Meeting of the Society of Avian Paleontology and Evolution*, ed. W.E. Boles and T.H. Worthy. *Records of the Australian Museum* 62(1): 145–155.

C.W. De Vis, of the Queensland Museum, named numerous fossil birds on the basis of specimens from the Darling Downs, southeastern Queensland, and the Cooper Creek/Warburton River region of South Australia (De Vis, 1888a,b, 1889, 1892, 1905). Although he was prolific, De Vis lacked more than a cursory reference collection, missing representatives of a number of the families to which he allocated taxa. He also held the belief that fossils could be related to, but had to be separate species from, living ones. Many of his taxa are still recognised, but a number of species have been found to be allocated to the wrong family, or to be junior synonyms of living species, or both (summarized by van Tets & Rich, 1990).

Most of his nominal species have been reviewed (megapodes: van Tets, 1974; ducks: Olson, 1977; pelicans: Rich & van Tets, 1981; storks: Boles, 2005; flamingos: Rich *et al*., 1987; birds of prey: Rich *et al*., 1982, Gaff, 2002; rails: Olson, 1975; pigeons: van Tets & Rich, 1980). Among the few that await detailed re-examination are the cormorants. De Vis (1905) erected two species from central Australian material, *Phalacrocorax gregorii* and *P. vetustus*, each on the basis of large syntypic series of assorted skeletal elements (Tables 1–8). He gave few details on the characters used to diagnose these species. Lambrecht (1933) created the genus *Australocorax* for them (type species *Phalacrocorax gregorii*). Cursory examination of the material led G.F. van Tets (pers. comm. in Condon, 1975) to suggest possible synonymy with the Pied Cormorant *Phalacrocorax varius*. Later, Rich & van Tets (1982), van Tets (1984) and van Tets & Rich (1990) considered that De Vis' series comprised composites of modern forms, the Pied Cormorant, Great Cormorant *P. carbo* and Black-faced Shag *P. fuscescens* (sometimes placed in the genus *Leucocarbo*) and, in the case of *vetustus*, the Darter *Anhinga novaehollandiae*, as well. Rich & van Tets (1982) provided a list of De Vis' fossil bird specimens, with an indication of proposed identifications. Each of the cormorant bones was tentatively associated with a living species. No indication was given in that list regarding the basis on which the specimens were attributed to which taxa, and, although reference is made to "van Tets & Rich, in prep", this has not been published subsequently.

Owing to van Tets' longstanding interest in cormorants, both fossil and living, it is very likely that he was responsible for most, if not all, of these specific allocations. Annotated labels accompanying specimens in the Queensland Museum collection cite his identifications. In addition, an unpublished manuscript by van Tets in the Australian National Wildlife Collection, Canberra, gives some insight into his thinking, although it does not provide the characters for his species identification. He noted that De Vis' reference collection apparently contained only *P. carbo* and Little Black Cormorant *P. sulcirostris* (which appears to have had significant ramifications in the descriptions of *gregorii* and *vetustus*). This manuscript was consulted during this study, but a number of the conclusions differ.

One of the most interesting, and controversial, aspects of van Tets' identifications is the allocation of some specimens to *P. fuscescens*, an exclusively marine species (Marchant & Higgins, 1990). Its presence in central Australia would be unexpected, but if valid, could have resulted from an isolated population associated with a marine incursion into this low lying region. Alternatively, according to Rich & van Tets (1982), "It appears that there may have been a land-locked population of a *Leucocarbo* similar to the Black-faced Shag in the Lake Eyre Basin during the Pleistocene, analogous to that of the almost land-locked European Shag, *Stictocarbo aristotelis* in the Mediterranean, and an extinct, small gannet, *Morus*, in the Black Sea".

The aims of this study are (*a*) to identify and allocate these bones to the correct species, where possible, and, (*b*) if there are no unnamed fossil forms represented, synonymize De Vis' cormorants with living ones by designating a lectotype for each.

Geology and geographic setting. Almost all of the specimens considered here were collected on J.W. Gregory's 1901–1902 trip to central Australia, along the Cooper Creek and Warburton River, northeastern South Australia (Gregory, 1906; Fig. 1). Specific site names were cited by De Vis (1905) for many of the specimens, but others have no more general location than "Lower Cooper Creek". Tedford & Wells (1990) were able to locate many of Gregory's place names, but others could not be found on his map, so their precise localities could not be confirmed. Various, but phonetically similar, spellings were used for several sites by Gregory (see discussion in Tedford & Wells, 1990) and apparently repeated by De Vis in his descriptions. Malkuni (or Malkuni Waterhole; also Mulcani), also known as Emu Camp, is a well established locality along the Cooper. Wurdulmankula (also written as Wurdumankula and Wurdumulankula) and Wankameminna, as well as those given only as Lower Cooper, could not be determined by Tedford & Wells (1990). The Kalamurina locality of Gregory is near the old Kalamurina Homestead along the Warburton River.

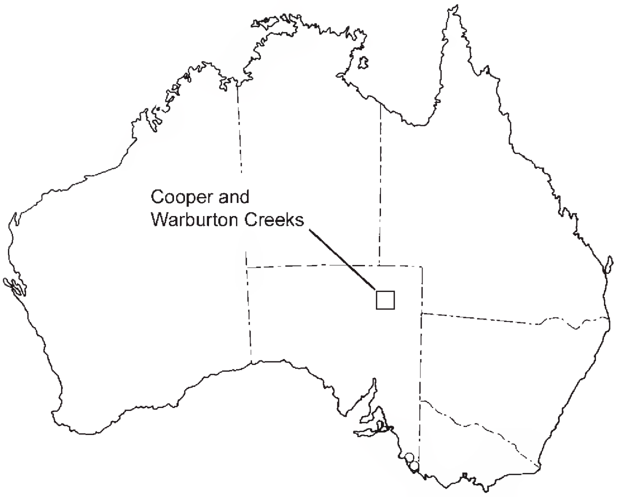

Figure 1. Location of portions of Cooper and Warburton Creeks, South Australia, relevant to this study.

A maxilla described by De Vis was collected by the Government Geologist, H.Y.L. Brown. De Vis cited the locality as "(?)", whereas Rich & van Tets (1982) gave it as Cutupirra (= Katipiri = Kutipirra) on Cooper Creek. Brown's collections, however, were made on a stretch of the Warburton River, including the Kalamurina area (Brown, 1892).

Tedford & Wells (1990) recognized that the fossil material from these Cooper Creek sites represented two faunas: the Malkuni Fauna from the Katipiri Formation and the slightly older Lower Cooper Creek Fauna from the Kutjitara Formation, while those at the Warburton River were part of the Kalamurina Fauna; all represent primarily fluviatile accumulations. The fossils considered in this paper come from the Middle to Late Pleistocene Katipiri Formation. This comprises mostly unconsolidated, fine white sand, with interspersed mud drapes accumulated during several episodes of deposition. The deposits overlie or are partly incised into the older Tirari and Kutjitara Formations.

Many specimens of the Malkuni Fauna were found as "float" on sandbars or river bed in the watercourse, while others occurred at the base of cliff in which the Katipiri Formation is exposed. The mammalian fauna was a mixture of now extinct taxa, such as diprotodontids, and living forms, such as koalas *Phascolarctos* and Agile Wallabies *Macropus agilis* found today in eastern and northern parts of the continent, respectively. For more detailed discussion of the geology and faunas of this region, see Stirton *et al.* (1961), Lundelius (1983), Woodburne *et al.* (1985), Tedford *et al.* (1986); Tedford & Wells (1990); Nanson *et al.* (2008); and references therein.

Materials and methods

The De Vis specimens are housed in the Queensland Museum, with the exception of P18413 (premaxillary) held in the South Australian Museum. Morphological characters were taken from Owre (1967), Ono (1980), Gilbert *et al.* (1981) and Siegel-Causey (1988) and from direct comparisons of specimens. Institutional prefixes to registration numbers of comparative material used in this study are AM (Australian Museum), ANWC (Australian National Wildlife Collection), MV (Museum Victoria) and SAM (South Australian Museum). Terminology of bones largely follows Baumel & Witmer (1993). Measurements follow the methods illustrated by Steadman (1980) and were made with digital calipers accurate to 0.01 mm and rounded to the nearest 0.1 mm. A number of De Vis' specimens are broken, thus often rendering the comparative measurements inapplicable, requiring direct comparisons with reference skeletons by eye. Scientific names of Australian species follow Christidis & Boles (2008).

Systematic paleontology

Also described from Cooper Creek is the fossil darter *Plotus laticeps* De Vis, 1905. This was subsequently synonymized with the extant *Anhinga novaehollandiae* (Mackness & van Tets, 1995). Cormorants and darters are similar osteologically, but exhibit consistent differences in major elements so that separation is possible for sufficiently intact bones. Differentiating the species of cormorants found in Australia is more reliant on size than morphological features in these quite osteologically uniform birds. The size sequence, from largest to smallest, is *Phalacrocorax carbo, varius, fuscescens, sulcirostris* and *Microcarbo melanoleucos* (Little Pied Cormorant); the last two are markedly smaller-bodied birds than *P. gregorii* and *P. vetustus* and are not of further concern here. Other than *melanoleucos*, Australian cormorants are dimorphic in size, with males being the larger sex. There is usually a small to moderate degree of overlap in size between the female of the larger species and the male of the next species in the sequence; for example, see Fig. 2, which illustrates these relative sizes for the proximal femur. Other features, such as comparative robustness of the bones, are useful for specimens in this range of overlap.

In the following consideration and re-evaluation of the specimens, a few characters for the separation of *Anhinga* and *Phalacrocorax* are presented first, followed by criteria for distinguishing the species of cormorants; these are characters sufficient to separate taxa, but are not exhaustive. In almost all cases where there is a potential question about the identity of a specimen, it is one between *carbo* and *varius* or *varius* and *fuscescens*. Finally, the determinations of the fossils from this study are given, with discussion of those that disagree with the assignments in Rich & van Tets (1982).

Premaxillary. SAM P18413, the only specimen held other than at the Queensland Museum, consists of an entire maxilla from the tip to the nasofrontal hinge. It is easily identified as that of a cormorant rather than of a darter by having the tip hooked, rather than straight and pointed. De Vis cited the locality as "(?)", whereas Rich & van Tets (1982) give it as Cutupirra on Cooper Creek. De Vis stated that it most closely resembled *P. carbo* and, indeed, "its non-identity with the living cormorant of southern waters depends on that or the numerous bones associated with it". Rich & van Tets (1982) gave the identification as *varius*.

The specimen is 78.5 mm from the tip to the nasofrontal hinge; the width at the hinge is 15.9 mm. The length falls in the overlap zone between *carbo* and *varius*. The latter, however, is proportionally thinner (13.5–16.4 mm) than *carbo* (16.7–17.5 mm). The maxilla of *gregorii* is within the range of *varius* and is here considered to belong to that species, confirming the identification by Rich & van Tets (1982).

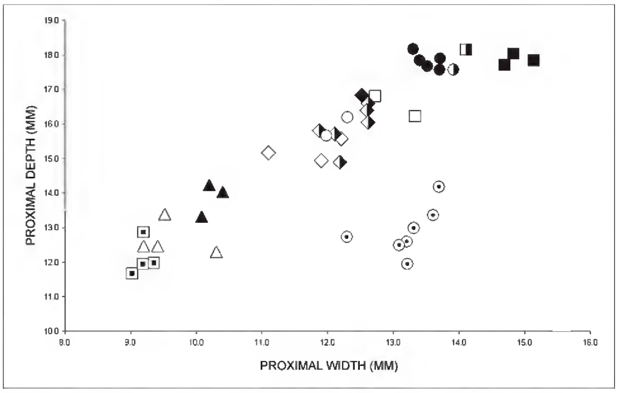

Figure 2. Measurements of the proximal end of the femur for extant Australian species of cormorant *Phalacrocorax* illustrating sexual size dimorphism within species and overlap between species. Species: squares, *Phalacrocorax carbo*; circles, *P. varius*; diamonds, *P. fuscescens*; triangles, *P. sulcirostris*; square with dot, *P. melanoleucos*; circle with dot, *Anhinga novaehollandiae*. Sex: males, black; females, white; unsexed, half and half.

Coracoid (Table 1). *Phalacrocorax* is separated from *Anhinga* by having the facies articularis sternalis strongly lipped on the ventral surface. *Phalacrocorax carbo* and *varius* differ mainly in size, rather than morphology, with some overlap between females of the former and males of the latter. *Phalacrocorax varius* differs from *fuscescens* by having the sternal end of the facies articularis humeralis wider (Fig. 3).

gregorii—De Vis assigned two coracoidal specimens to this species. Most of his description was devoted to a fragment of the humeral end (F3755). Although it was "about the same size as in *P. carbo*", De Vis remarked that it "conspicuously differs in the size and form of the facets for the humerus and, particularly, the scapula, which is a deep cup-shaped cavity, occupying the entire articular surface of the procoracoid process". These and other characters presented are unlike *carbo* for a good reason: this bone (F3755) is, in fact, from a heron (Ardeidae), as was recognized by Rich & van Tets (1982). This identification was confirmed, the Ardeidae being separated from the Phalacrocoracidae and Anhingidae by the combination of having the processus procoracoideus triangular (small rounded bump in Phalacrocoracidae and Anhingidae), cotyla scapularis round and deep (obsolete), impressio lig. acrocoracoideum wide and rectangular (narrow, extending far sternally), sulcus m. supracoracoideus very broad, not bounded by ridges on sides, bordered

Table 1. Coracoids of De Vis' cormorants, with localities and specific identifications according to Rich & van Tets (1982) and this study. Abbreviations: end, *c*, complete; *h*, humeral; *st*, sternal; side: *l*, left; *r*, right.

QM no.	end	side	locality	Rich & van Tets (1982)	this study
Phalacrocorax gregorii					
F3754	st	r	Lower Cooper	*carbo*	*carbo*
F3755	h	r	Wankameminna	Ardeidae	Ardeidae (large)
Phalacrocorax vetustus					
F3789	p	r	Malkuni	*carbo*	*varius*
F3790	h	r	Malkuni	*fuscescens*	*varius*
F3791	st	l	Kalamurina	*fuscescens*	*varius*

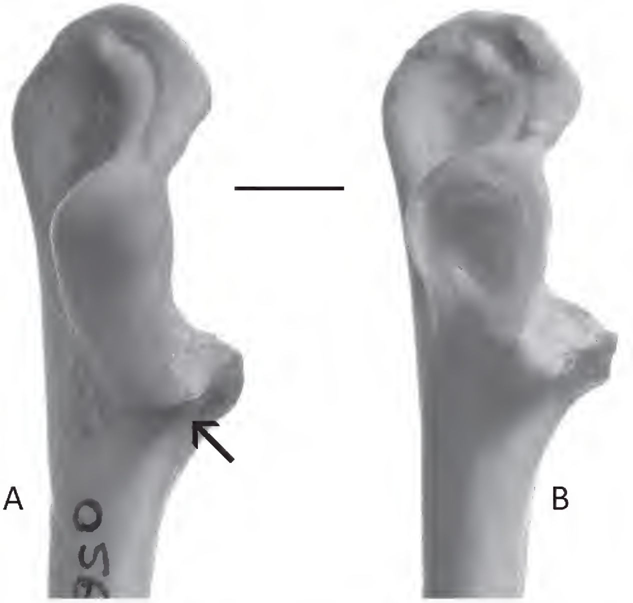

Figure 3. Shoulder end of coracoid (dorsolateral view) showing differences in the width of the sternal end of facies articularis humeralis between (*A*) *Phalacrocorax varius* and (*B*) *P. fuscescens*.

humerally by the more or less flat edge of facies articularis clavicularis (narrow and elongate, bounded on sides, pointed humerally). F3755 comes from a large heron. In his unpublished manuscript, van Tets referred it to the Large-billed Heron *Ardea sumatrana*, Australia's largest bodied heron. The size of this fossil is comparable to the Great Blue Heron *A. herodias* of the New World (Fig. 4). A taxonomic allocation of this specimen to *A. sumatrana* raises more questions than those arising from the putative presence of *P. fuscescens*. *Ardea sumatrana* occurs along the coasts of northern Australia, New Guinea and western Indonesian islands, where it is almost exclusively a bird of mangroves.

vetustus—Regarding the coracoid of this species, De Vis remarked, "The unlikeness of this to the coracoid of *P. gregorii* is great". Again, because of the misidentification of the latter, this is not surprising. Of the three specimens, Rich & van Tets (1982) listed one as *carbo* and the other two as *fuscescens*. Re-examination indicates that all can be referred to *varius*. The size of F3789 is more indicative of this species than *carbo* and the other two specimens are distinguished from *fuscescens* by the characters given above.

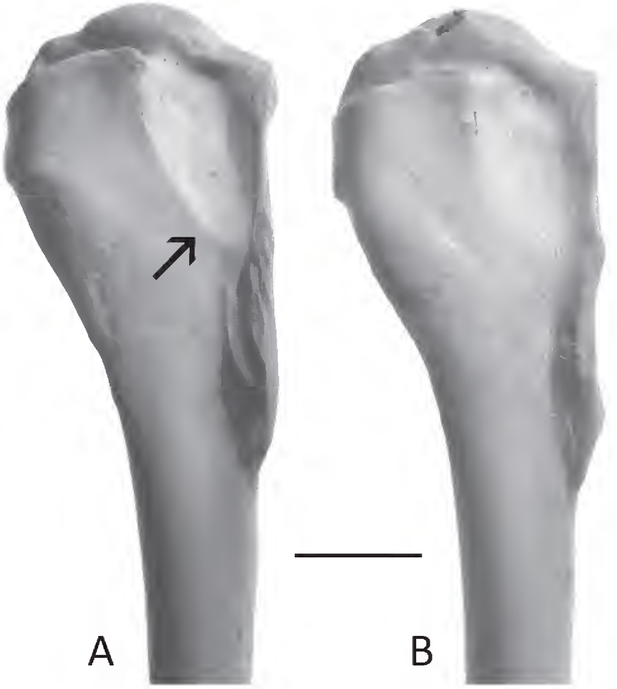

Figure 5. Proximal end of humerus (cranial view) showing differences in distal delimitation of the impressio coracobrachialis in (*A*) *Phalacrocorax fuscescens* and (*B*) *P. varius*.

Humerus (Table 2). Cormorants differ from darters by having the fossa pneumotricipitalis deeper proximally, tuberculum dorsale forming a sharp angle (rather than rounded) and impressio coracobrachialis proportionally narrower (in *Anhinga*, this comprises 50% or more of cranial face of the proximal end). Rich & van Tets (1982) did not refer any humeral specimens to *Anhinga*.

Size is a good distinguishing character for some species, with male *carbo* being detectably larger than other taxa. For the two smaller species, *fuscescens* can be separated

Table 2. Humeri of De Vis' cormorants, with localities and specific identifications according to Rich & van Tets (1982) and this study. Abbreviations: end: *p*, proximal; *s*, shaft; *d*, distal; side: *l*, left; *r*, right.

QM no.	end	side	locality	Rich & van Tets (1982)	this study
Phalacrocorax gregorii					
F3756	p	l	Malkuni	*carbo*	*carbo*
F3757	d+s	r	Kalamurina	*carbo*	*carbo*
F3758	d+s	r	Lower Cooper	*carbo*	*carbo*
F3759	d	r	Lower Cooper	*carbo*	*carbo*
F3760	s	r	Malkuni	*carbo*	*carbo*
F3761	d	l	Malkuni	*carbo*	*carbo*
F3762	d	l	Lower Cooper	*carbo*	*varius*
Phalacrocorax vetustus					
F3792	p	l	Malkuni	*fuscescens*	*varius*
F3793	p	l	Malkuni	*fuscescens*	*varius*
F3794	p	l	Malkuni	*fuscescens*	*varius*
F3795	d	l	Kalamurina	*fuscescens*	*varius*
F3796	d	l	Malkuni	*varius*	*varius*
F3797	d	r	Lower Cooper	*carbo*	cf. *carbo*

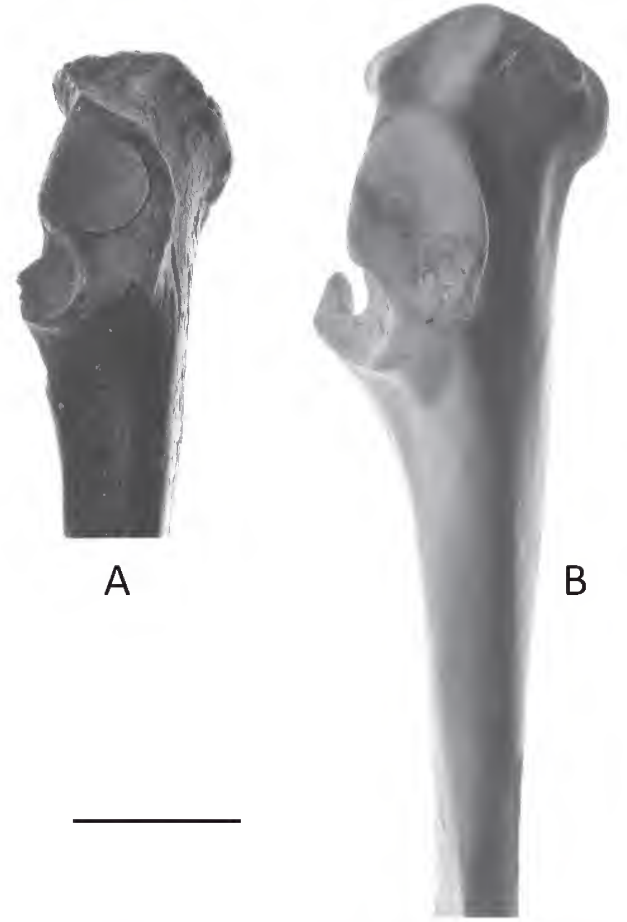

Figure 4. Shoulder end of coracoid (dorsal view) showing similarities in morphology and size between (*A*) QM3755 and (*B*) *Ardea herodias*.

from *varius* by the depth and distal extent of the impressio coracobrachialis (Fig. 5). In *fuscescens* it is deep and terminates abruptly with a marked distal border, whereas in *varius* the impressio is shallower with the distal border low and merging more smoothly into the shaft. The distal end of *varius* differs from those of both *carbo* and *fuscescens* by having the fossa m. brachialis more excavated, particularly on the ventral side such that its border is much more prominent (Fig. 6).

gregorii—All the specimens except F3762 can be identified as *carbo* based on size and morphology. F3762 is referred to *varius*, rather than *carbo*, by the structure of the fossa m. brachialis (see above).

vetustus—Three proximal fragments of *vetustus* (F3792–4) were considered by Rich & van Tets (1982) to belong to *fuscescens*. They are here placed with *varius* on the condition of the impressio coracobrachialis. A distal fragment (F3795) was also considered to be *fuscescens* by Rich & van Tets (1982) but exhibits the deeper fossa m. brachialis of *varius*. A specimen of a young bird not fully ossified (F3797) retains a portion of shaft that is slightly more robust than in *varius* and shows less curvature; its reidentification by Rich & van Tets (1982) as *carbo* is tentatively confirmed. Another specimen, a right distal fragment from Kalamurina assigned to *vetustus*, was lost subsequent to the description by De Vis (1905) and thus not registered in the Queensland Museum collection.

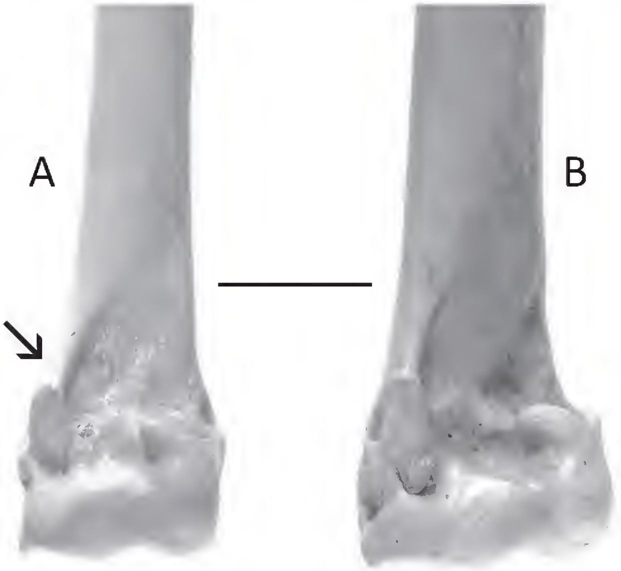

Figure 6. Distal end of humerus (cranial view) showing differences in excavation of the fossa m. brachialis in (*A*) *Phalacrocorax varius* and (*B*) *P. carbo*.

Ulna (Table 3). The proximal end of the cormorant ulna differs from that of the darter's by having the cotyla dorsalis broader (proximal view) and the processus cotylaris dorsalis with a prominent triangular, dorsodistally directed projection.

The character states listed by Siegel-Causey (1988) indicated that the attachment of M. bicipitis connects the depressio m. brachialis by a strong ridge in *varius* but these are separate in *fuscescens*; this could not be confirmed. Characters of the proximal end by which these species can be separated are, in *varius*, the proximal end of the depressio m. brachialis is deeper, extending further proximally and undercutting the tuberculum lig. collateralis ventralis; in *fuscescens*, the sulcus tendineus is deeper throughout its extent with more sharply defined borders and the tuberculum lig. collateralis ventralis projects further cranially. Compared to that of *varius*, the ulna of *carbo* is more robust, on the proximal end notably in the development of the olecranon.

vetustus—De Vis referred no ulnar specimens to *gregorii* but placed two proximal fragments with *vetustus*. Unfortunately, damage to the both specimens prevents any of the preceding

Table 3. Ulnae of De Vis' cormorants, with localities and specific identifications according to Rich & van Tets (1982) and this study. Abbreviations: end: *p*, proximal; side: *r*, right.

QM no.	end	side	locality	Rich & van Tets (1982)	this study
Phalacrocorax vetustus					
F3798	p	r	Malkuni	*fuscescens*	cf. *varius*
F3799	p	r	Wurdumankula	*fuscescens*	cf. *varius*

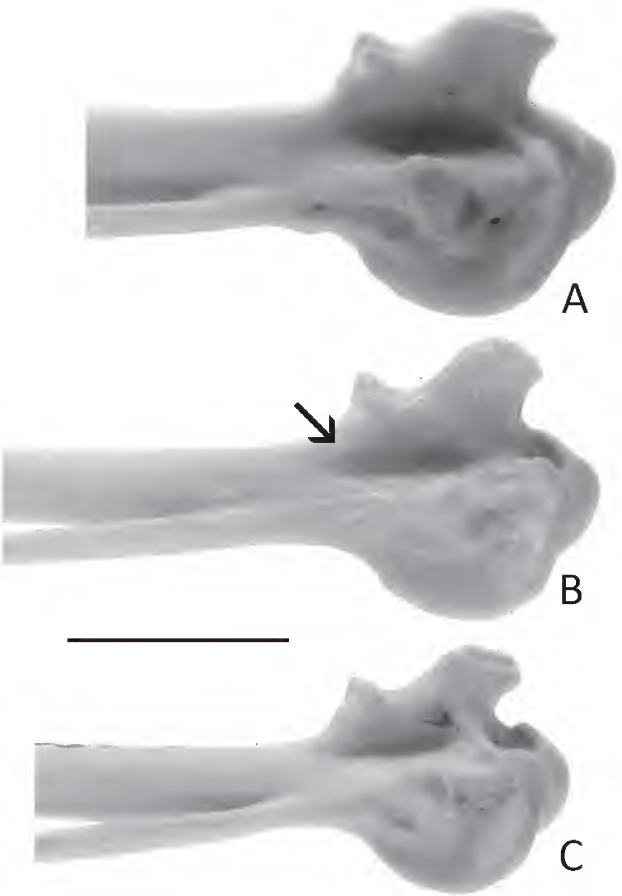

Figure 7. Proximal end of the ventral side of the carpometacarpus (ventral view) showing differences in excavation for the insertion of M. flexor digiti II in (*A*) *Phalacrocorax carbo*, (*B*) *P. varius* and (*C*) *P. fuscescens*.

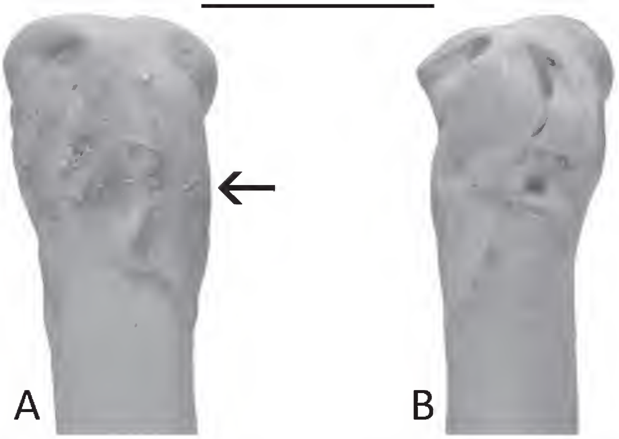

Figure 8. Proximal end of femur (lateral view) showing differences in development of the cranial border of the facies articularis antitrochantericus between (*A*) *Phalacrocorax* and (*B*) *Anhinga*.

characters being assessed with confidence. What structures remain, however, show greater resemblance to the conditions in *varius*, and these specimens are tentatively referred to that species.

Carpometacarpus (Table 4). In *Phalacrocorax*, the processus pisiformis is situated at the centre of the ventral side of the trochlea carpalis, whereas in *Anhinga* it is distal to this midpoint. Cormorants also have a deeply incised fovea carpalis cranialis, whereas this feature is absent in *Anhinga*.

Cormorants have an excavation on the ventral side of the proximal cranial to the processus pisiformis for the insertion of M. flexor digiti II. In addition to its larger size, *carbo* can be recognized by having this excavation deeper (Fig. 7B). In *fuscescens*, this is excavation extends cranially into the base of the processus extensorius (Fig. 7A). Compare these states with that of *varius* (Fig. 7C) in which the excavation is shallower and lacks the cranial extension.

gregorii—Both specimens, placed with *carbo* by Rich & van Tets (1982), agree with that species in size and morphology.

vetustus—Although F3800 falls into an area of overlap in size between *fuscescens* and *varius*, the structure of the insertion of M. flexor digiti II and the overall robustness indicate that it represents the latter species. The distal fragment F3801 is on size either a female *carbo* or male *varius*; an assignment cannot be made with confidence. F3802, a proximal end, is also intermediate in size between these species; abrasion to the ventral side prevents positive assessment of the degree of excavation but it appears to be more similar to *varius*.

Femur (Table 5). Cormorants have the craniocaudal expansion of the lateral side of the proximal end, notably that caused by the cranially expanded crista trochantericus femoris, very obvious in lateral view (Fig. 8), and the cranial border of the facies articularis antitrochantericus is well pronounced, delimiting the proximal end from the cranial face of the shaft (Fig. 9). In *Anhinga*, there is little expansion of the crista trochantericus femoris nor is the facies articularis antitrochantericus strongly bordered on its cranial side. On

Table 4. Carpometacarpi of De Vis' cormorants, with localities and specific identifications according to Rich & van Tets (1982) and this study. Abbreviations: end: *c*, complete; *p*, proximal; *d*, distal; side: *l*, left; *r*, right; sex: *M*, male; *F*, female.

QM no.	end	side	locality	Rich & van Tets (1982)	this study
Phalacrocorax gregorii					
F3763	c	r	Lower Cooper	*carbo*	*carbo*
F7020	p	r	Malkuni	*carbo*	*carbo*
Phalacrocorax vetustus					
F3800	p	r	Wurdumankula	*fuscescens*	*varius*
F3801	d	l	Lower Cooper	*carbo*	*carbo* F / *varius* M
F3802	p	l	Malkuni	*carbo*	cf. *varius*
F3803	c	r	Lower Cooper	*varius*	*varius*

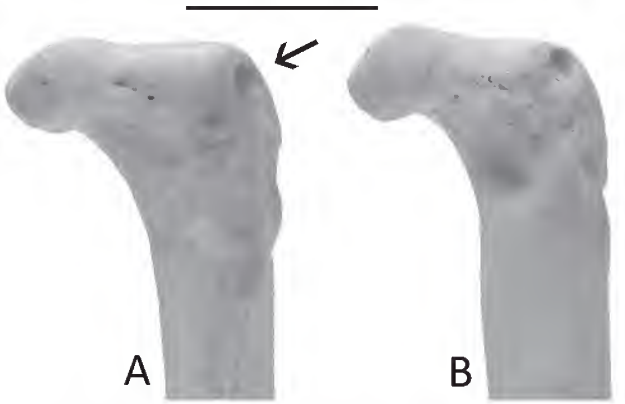

Figure 9. Proximal end of femur (cranial view) showing differences in extent of craniocaudal expansion of the trochanteric region between (*A*) *Phalacrocorax* and (*B*) *Anhinga*.

the distal end (Fig. 10), the trochlea fibularis is more robustly developed in *Phalacrocorax* and the attachment for M. flexor hallicus longus is expressed as a deep depression lateral and proximal to the condylus lateralis and proximal to the trochlea fibularis (depression small or absent in *Anhinga*).

The only apparent differences among the species of cormorants are ones of size.

gregorii—Rich & van Tets (1982) assigned specimen F3767 to *Anhinga laticeps* (De Vis, 1905) (now synonymized with the living *Anhinga novaehollandiae*: Mackness & van Tets, 1995). It exhibits the craniocaudal expansion of the proximal end characteristic of *Phalacrocorax*. On the basis of size, it should be considered *P. carbo*. Of the two specimens placed in *fuscescens*, F3769 agrees with *varius* on size while F3768 falls into the *varius–fuscescens* overlap zone. Although the latter cannot be confirmed with confidence, it is here considered to be more likely a small individual of *varius*.

vetustus—The two largely complete specimens were regarded by Rich & van Tets (1982) to be *fuscescens*. They fall into the overlap zone of size between male *fuscescens* and female *varius*. As with the specimen discussed above, these are more probably small *varius*.

Tibiotarsus (Table 6). In cranial view, the epicondylus medialis extends further beyond the medial margin in *Phalacrocorax* and the distal end of the shaft lateral to the proximal opening of the sulcus extensorius is more expanded laterally in *Phalacrocorax*. In cranial view, the crista cnemialis medialis is directed cranially in *Phalacrocorax*, rather than craniolaterally, as in *Anhinga*.

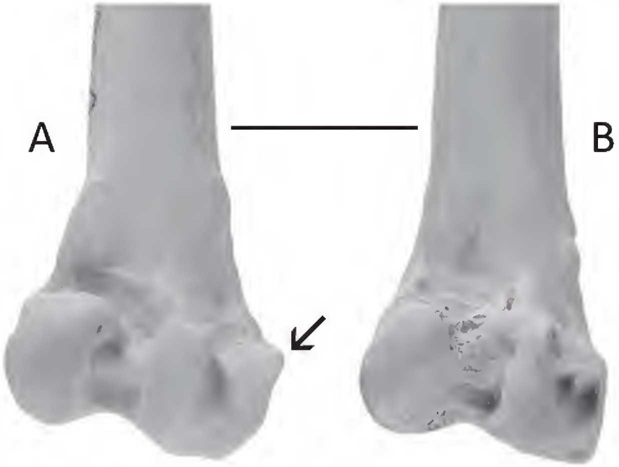

Figure 10. Distal end of femur (caudal view) showing differences in robustness of the trochlea fibularis between (*A*) *Phalacrocorax* and (*B*) *Anhinga*.

Overall size and robustness of this element serve to distinguish the species of cormorants.

gregorii—While the three distal fragments are considered to be *varius* by Rich & van Tets (1982) and this study, the fourth specimen (F3771) is in the overlap zone between *varius* and *carbo* and cannot be placed unequivocally in either.

vetustus—The placement by Rich & van Tets (1982) of both specimens with *varius* is confirmed here on the basis of size.

Tarsometatarsus (Table 7). This element in *Anhinga* is proportionally shorter with a stouter shaft, more splayed distal end, a trochlea metatarsi III that projects further distally than trochlea metatarsi IV but not as far as trochlea metatarsi II. *Phalacrocorax varius* has a more gracile shaft than either *carbo* or *fuscescens*, even in zones of size overlap, and the raised area on the plantar surface bounded by the lineae intermusculares is narrower (broader and flatter in *carbo*).

gregrorii—F3775 and F3776 were referred to *carbo* by Rich

Table 5. Femora of De Vis' cormorants, with localities and specific identifications according to Rich & van Tets (1982) and this study. Abbreviations: end: *c*, complete; *p*, proximal; side: *l*, left; *r*, right; sex: *M*, male; *F*, female.

QM no.	end	side	locality	Rich & van Tets (1982)	this study
Phalacrocorax gregorii					
F3764	c	l	Malkuni	*carbo*	*carbo*
F3765	c	l	Wurdamankula	*carbo*	*carbo*
F3766	c	l	Wurdamankula	*varius*	*varius*
F3767	c	l	Wurdamankula	*Anhinga* [*laticeps*]	*carbo*
F3768	p	l	Lower Cooper	*fuscescens*	*varius* F / *fuscescens* M
F3769	p	r	Malkuni	*fuscescens*	*varius*
F3770	p	l	Malkuni	*carbo*	*carbo*
Phalacrocorax vetustus					
F3804	c	r	Malkuni	*fuscescens*	*varius* F / *fuscescens* M
F3805	c	l	Lower Cooper	*fuscescens*	*varius* F / *fuscescens* M

Table 6. Tibiotarsi of De Vis' cormorants, with localities and specific identifications according to Rich & van Tets (1982) and this study. Abbreviations: end: *p*, proximal; *d*, distal; side: *l*, left; *r*, right.

QM no.	end	side	locality	Rich & van Tets (1982)	this study
Phalacrocorax gregorii					
F3771	p	r	Malkuni	*varius*	*carbo*/*varius*
F3772	d	r	Lower Cooper	*varius*	*varius*
F3773	d	l	Lower Cooper	*varius*	*varius*
F3774	d	l	Malkuni	*varius*	*varius*
Phalacrocorax vetustus					
F3806	p	l	Malkuni	*varius*	*varius*
F3807	p	r	Malkuni	*varius*	*varius*

& van Tets (1982) but are here regarded as *varius* on the basis of their gracility. Although he listed them in his description, De Vis thought it doubtful that two specimens (F3779 and F3780) belonged to this species. "If they do, this cormorant must have varied very much in size. The last especially has an unwontedly massive appearance." Here both are referred to *P. carbo*.

vetustus—For the only tarsometatarsus he assigned to this species, De Vis noted that "The proportions of this bone are the only means of determining its place to be in the present species" (De Vis, 1905), the length and least width being less than *P. gregorii* and *P. carbo*. Rich & van Tets (1982) referred it to *fuscescens*; however, the bone's gracility and the narrowness of the plantar area between the lineae intermusculares indicate that it should be assigned to *varius*.

Pelvis (Table 8). The crista iliaca dorsalis of *Anhinga* continues from the midline along the caudal border of the alae preacetabular ilii; in *Phalacrocorax* there is no caudal ridge, the alae merging smoothly into the acetabular region of the pelvis (Fig. 11). The synsacrum in *Anhinga* is more robust through the acetabular region, particularly ventrally, such that, in lateral view, it is visible through the acetabulum, occupying most of the space; it covers 50% of this space at most in cormorants (Fig. 12).

gregorii—De Vis placed eight pelvic fragments in *gregorii* and none in *vetustus*. There are several disagreements between Rich & van Tets (1982) and this study. Two specimens are in the overlap zone for *fuscescens* and *varius* but are likely to be the latter. One also falls into a similar intermediate region for *carbo* and *varius*. The distance across the antitrochanters in F3786 indicates that this specimen is *varius*, not *carbo*.

Discussion and results

De Vis appears to have worked under the assumption that any fossil had to represent a different species than one living, although it could be closely related. This outlook undoubtedly contributed to his recognition of the numerous fossil taxa that have now been synonymized with modern species. Additionally, his small reference collection would have been an important factor in the case of cormorants. By having only the largest species and one smaller than all taxa in the fossil sample, many specimens could not be matched and so would appear as new. Indeed, De Vis makes many of his comparisons with *P. carbo* and explicitly cites size as a diagnostic character for several specimens.

The syntypic series of *P. gregorii* is a mixture of *P. carbo* and *P. varius*, with a very minor component of *Anhinga novaehollandiae* and a heron. A number of skeletal elements of the first two species cannot be separated except on size and, even then, there is a range of overlap between them. The range of size variation even within a species could not have been discerned with De Vis' restricted number of comparative samples.

Likewise, this was undoubtedly a confounding factor in the recognition of *P. vetustus*. For example, De Vis characterized this species as "a Cormorant of smaller size and slighter build than *P. gregorii* or *P. carbo*, about intermediate between them and *P. stictocephalus* [= *sulcirostris*]". This succinct circumscription provides a good characterization of

Table 7. Tarsometatarsi of De Vis' cormorants, with localities and specific identifications according to Rich & van Tets (1982) and this study. Abbreviations: end: *c*, complete; *p*, proximal; *s*, shaft; *d*, distal; side: *l*, left; *r*, right.

QM no.	end	side	locality	Rich & van Tets (1982)	this study
Phalacrocorax gregorii					
F3775	d	l	Malkuni	*carbo*	*varius*
F3776	c	r	Wurdamankula	*carbo*	*varius*
F3777	p	l	Malkuni	*varius*	*carbo*
F3778	p+s	r	Lower Cooper	*varius*	*varius*
F3779	c	l	Lower Cooper	*carbo*	*carbo*
F3780	c	r	Lower Cooper	*varius*	*carbo*
Phalacrocorax vetustus					
F3808	s	l	Lower Cooper	*fuscescens*	*varius*

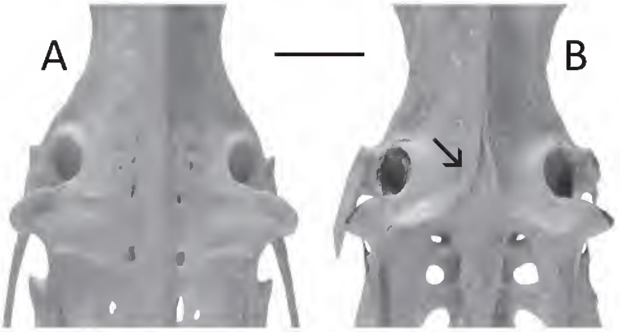

Figure 11. Pelvis (dorsal view) showing differences in development of the crista iliaca dorsalis between (*A*) *Phalacrocorax* and (*B*) *Anhinga*.

P. varius, which is smaller and more gracile than *P. carbo* but larger than *P. sulcirostris*. It is not surprisingly, then, that most of the syntypic specimens of *P. vetustus* can be referred to *P. varius*.

No incontrovertible evidence of *P. fuscescens* could be found. Almost all specimens considered by Rich & van Tets (1982) to be this species can be referred to *P. varius*. A few fall into an area of intermediacy of size or morphology and their identifications must remain inconclusive. There is no reason to invoke the presence of *fuscescens* for these in the absence of any other evidence, whereas *varius* is well represented among the remaining specimens. This also makes much more sense on distributional grounds and habitat preferences. A wide-ranging species with broad ecological tolerances is a more acceptable choice than one restricted to marine habitats along continental coasts until evidence demonstrates otherwise.

The humeral end of a coracoid (F3755) represents a large heron. Rich & van Tets (1982) correctly identified this as Ardeidae but did not make a finer taxonomic resolution. In van Tets' unpublished manuscript, he had decided that this represented the largest Australian species, *Ardea sumatrana*. This species is mangrove-specialist of the northern coast line. That such a species would be found in the waterways of central Australia during the Quaternary is most unlikely. Nonetheless, the specimen is larger than that of any other living Australian heron. It seems more probable that this might be evidence of a large, now extinct and unnamed species of heron. No specific level identification is offered here.

De Vis (1905) did not designate a holotype for either taxon. Below lectotypes are selected for *gregorii* and *vetustus*, which will serve to place these putative taxa into the synonymy of living species.

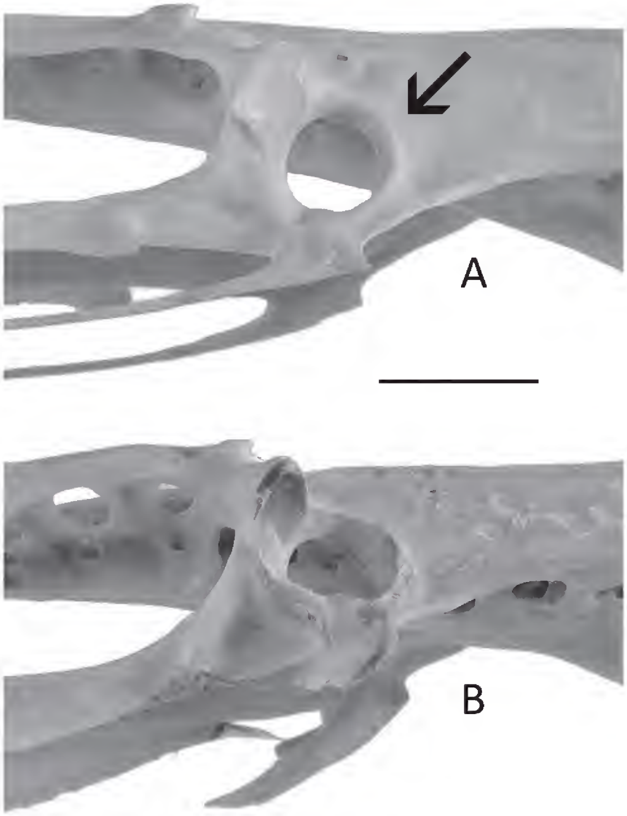

Figure 12. Pelvis (lateral view) showing differences in extent of the synsacrum visible through the acetabulum between (*A*) *Phalacrocorax* and (*B*) *Anhinga*.

The lectotype of *Phalacrocorax gregorii* is here designated to be F3756, a proximal humeral fragment, which is illustrated by De Vis (1905, plate VII, fig. 2A, B). As this has been identified as belonging to *P. carbo, P. gregorii* becomes a junior synonym of that species. Other specimens among the type series that are also considered here to be *carbo* become paralectotypes ([coracoid] F3754, [humerus] F3757, F3758, F3759, F3760, F3761, [carpometacarpus] F3763, F7020, [femur] F3764, F3765, F3767, F3770, [tarsometatarsus] F3777, F3779, F3780, [pelvis] F3784, F3786). The remaining fossils are either *P. varius* or *Anhinga novaehollandiae* and no longer have any

Table 8. Pelvic fragments of De Vis' cormorants, with localities and specific identifications according to Rich & van Tets (1982) and this study. Abbreviations: *s*, synsacrum; *a*, acetabulum; *2a*, both acetabula present; sex: *M*, male; *F*, female.

QM no.	portion	locality	Rich & van Tets (1982)	this study
Phalacrocorax gregorii				
F3781	s+2a	Lower Cooper	*varius*	*varius*
F3782	s+a	Lower Cooper	*varius*	*varius*
F3783	s+a	Lower Cooper	*fuscescens*	*varius / fuscescens*
F3784	a	Lower Cooper	*carbo*	*carbo*
F3785	s	Lower Cooper	*carbo*	*varius* M / *carbo* F
F3786	s+2a	Mulcani	*varius*	*carbo*
F3787	s+2a	Wurdumankula	*Anhinga*	*Anhinga*
F3788	s	Kalamurina	*fuscescens*	*varius / fuscescens*

nomenclatural status. The type locality for *P. gregorii* is restricted to Malkuni. The synonymization of *gregorii* with *carbo* is sensible because most of De Vis' specimens belong to the latter species and De Vis himself remarked several times on the similarity between the two.

Phalacrocorax vetustus is placed in the synonymy of *P. varius* by selecting as the lectotype F3792, a proximal humeral fragment, which is illustrated by De Vis (1905, plate VII, fig. 3A, B). The restricted type locality is also Malkuni; paralectotypes are [coracoid] F3789, F3790, F3791, [humerus] F3792, F3793, F3794, F3795, F3796, [carpometacarpus] F3800, F3803, [tibiotarsus] F3806, F3807, [tarsometatarsus] F3808. De Vis described *vetustus* as smaller and slighter than *gregorii*, which is a good characterization of *varius*.

As a result of this lectotypification, *Australocorax*, created by Lambrecht (1933) for these species (type species *Phalacrocorax gregorii*), becomes a junior synonym of *Phalacrocorax* Brisson, 1760.

Commenting on De Vis' cormorant specimens, Stirton *et al.* (1961) stated that "These materials should afford an opportunity to derive information on alterations in the distribution of the five living species of Australasian cormorant and they may contribute to our knowledge of the ecology, fresh water versus marine, of these birds". The reanalysis of these fossils indicates that two extant species were present. Both are widespread species across the continent, avoiding the drier parts of the inland, particularly in the western and southern halves where reliable water sources are absent. These cormorants still occur in the Cooper Creek and Warburton River, suggesting that the availability of open water there might not have been too different now as it was in the Late Pleistocene.

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The Upper Pliocene Avifauna of Ahl al Oughlam, Morocco. Systematics and Biogeography

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ABSTRACT. The locality of Ahl al Oughlam, situated at the southeastern limit of the city of Casablanca (Morocco) at about 34° north, is dated by the biochronology of its rich mammalian fauna to about 2.5 Ma. At the present time it is 6.5 km from the Atlantic Ocean but it was on the seashore when the fossil material was deposited. Among the seabirds are *Phoebastria anglica, Phoebastria* sp. cf. *P. albatrus, Phoebastria* sp. cf. *P. nigripes, Pelagornis mauretanicus, Calonectris* sp. cf. *C. diomedea, Morus peninsularis, Morus* sp. cf. *M. bassanus, Catharacta* sp. cf. *C. skua, Alca ausonia*. Among the landbirds are *Struthio asiaticus, Geronticus olsoni* n.sp., several anseriforms, *Plioperdix africana* n.sp., several otidids, *Agapornis atlanticus* n.sp., *Tyto balearica, T. alba, Surnia robusta*, and a few Passeriformes. The Recent species of albatrosses *Phoebastria albatrus* and *P. nigripes* live in the North Pacific but were also present in the North Atlantic until the Middle Pleistocene. The marine avifauna shows many similarities with that of the Yorktown Formation, in North Carolina. Unlike the mammals, which include many genera in common with the African faunas, the landbirds have more affinities with the Palaearctic region than with the Ethiopian region. They include several extinct genera or species that have been described, or identified, in the Pliocene of the Palaearctic region. The terrestrial avifauna is very different from all those that have been described from the upper Miocene and Pliocene of Africa.

RÉSUMÉ. Le gisement d'Ahl al Oughlam, situé à la limite sud-est de la ville de Casablanca (Maroc), à environ 34 ° de latitude Nord, est daté par la biochronologie de sa riche faune de mammifères d'environ 2,5 Ma. Il est actuellement situé à 6,5 km de l'Océan Atlantique mais il était sur le rivage de l'océan au moment où les fossiles ont été déposés. Parmi les formes marines on trouve *Phoebastria anglica, Phoebastria* sp. cf. *P. albatrus, Phoebastria* sp. cf. *P. nigripes, Pelagornis mauretanicus, Calonectris* sp. cf. *C. diomedea, Morus peninsularis, Morus* sp. cf. *M. bassanus, Catharacta* sp. cf. *C. skua*, et *Alca ausonia*. Parmi les formes terrestres on trouve *Struthio asiaticus, Geronticus olsoni* n.sp., plusieurs ansériformes, *Plioperdix africana* n.sp., plusieurs outardes, *Agapornis atlanticus* n.sp., *Tyto balearica, Tyto alba, Surnia robusta*, et quelques Passériformes. Les espèces actuelles d'albatros, *P. albatrus*, l'Albatros à queue courte, et *P. nigripes*, l'Albatros à pieds noirs, vivent actuellement dans le Pacifique Nord mais ont vécu aussi dans l'Atlantique Nord jusqu'au Pléistocène moyen. L'avifaune marine montre beaucoup de ressemblances avec celle de la Yorktown Formation, en Caroline du Nord. Contrairement aux mammifères, qui comportent beaucoup de genres en commun avec les faunes africaines, l'avifaune

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terrestre a plus d'affinités avec celle de la province paléarctique, qu'avec celle de la province éthiopienne. Elle comporte en particulier plusieurs genres ou espèces éteints, décrits ou identifiés dans le Pliocène de la province paléarctique. Cette avifaune terrestre est très différente de celles qui ont été décrites dans le Miocène supérieur ou le Pliocène d'Afrique.

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Introduction

The fossiliferous locality of Ahl al Oughlam [AaO] is an abandoned sandstone quarry located at the southeastern fringe of the city of Casablanca, Morocco, which will probably surround it in the near future (Fig. 1). Stratigraphically the quarry exhibits a maximum marine level which is 105 m above the present sea level, referred to as the Messaoudien in the local terminology. Above this marine level, fossils were discovered by J.-P. Raynal & J.-P. Texier in 1985 in a network of fissures and interconnected galleries within a consolidated dune (calcarenite). The locality was then excavated by Denis Geraads as part of the "Programme Casablanca" of the "Institut National des Sciences de l'Archéologie et du Patrimoine" (INSAP), under the direction of Fatima-Zohra Sbihi-Alaoui and Jean-Paul Raynal.

A survey of the vertebrate faunas was published by Geraads (2006). The mammalian fauna includes at least 55 species of both micro- and macro-mammals. The genus *Equus* is absent, implying that the site is older than about 2.3 Ma (Geraads, 2006). A new species of *Hipparion, H. pomeli*, has been described subsequently from the site (Eisenmann & Geraads, 2007). The vertebrate fauna also includes amphibians, reptiles (tortoises, crocodiles, amphisbaenids, lizards and snakes), and a few fish. The most unexpected element of the mammalian fauna is a walrus. No living or fossil walrus was previously known in the Eastern Atlantic, south of Belgium (Geraads, 2006). The site was formed in an oceanic Eulittoral environment which explains why both marine and terrestrial forms are found among the birds. The fissure fill is not stratified and, as the populations of the various rodent species from the different interconnected fissures do not significantly differ in tooth measurements, they can be considered as instantaneous at the geological scale. Although no absolute dating was possible, the biostratigraphical study of the mammals points to an age close to 2.5 Ma (Geraads, 2006).

A first published work on avifauna, describing the Struthioniformes and the Odontopterygiformes, was presented during the 2004 Sape Meeting, at Quillan (France) (Mourer-Chauviré & Geraads, 2008). The present work gives a complete systematic study of the avifauna.

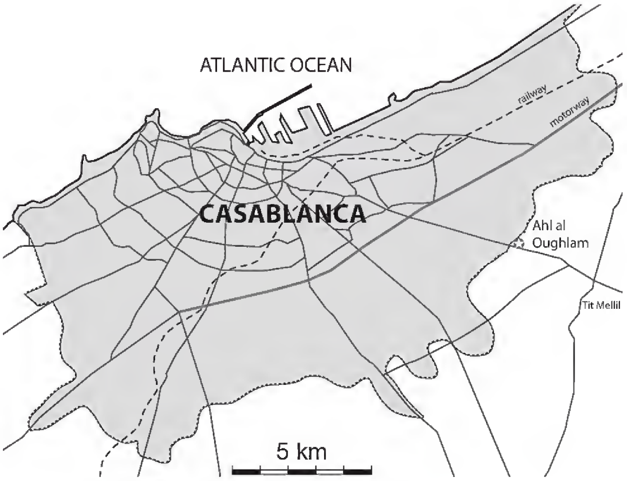

Figure 1. Map of the Casablanca urbanized area (in gray) with the location of the Ahl al Oughlam quarry (33°34'11"N 07°30'44"W).

Materials and methods

The highly calcareous sediments consist of loose clays with very friable bones and teeth, and concrete-hard breccias, from which bones and teeth were extracted by acid cleaning. Most of the bones, except the more robust ones, were crushed. All the material will be deposited in the collection of INSAP, at Rabat, Morocco, but casts of the most important material will be kept in the Université Claude Bernard, Lyon 1. The anatomical terminology generally follows Baumel & Witmer (1993) and, when necessary, Ballmann (1969) and Howard (1929). The biochronological stratigraphy (MN zones) follows Mein (1990). The comparative material comes from the collections of the National Museum of Natural History, Washington, D.C. (USNM); the Laboratoire d'Anatomie Comparée and the Institut de Paléontologie Humaine of the Muséum national d'Histoire naturelle, Paris (MNHN); the Paleontological Institute of the Russian Academy of Sciences, Moscow; and the Université Claude Bernard, Lyon 1 (UCB).

Systematic Paleontology

Order Struthioniformes

Family Struthionidae

Genus *Struthio* Linnaeus, 1758

Struthio asiaticus Milne-Edwards, 1871

Mourer-Chauviré & Geraads (2008) described material belonging to this species. *Struthio asiaticus* is an ostrich characterized by its massive proportions, in particular the proportions of phalanx 1 of posterior digit III. This phalanx is more massive than that of the Recent species *S. camelus*. At Ahl al Oughlam the bones are associated with fragments of eggshells of struthioid type. The thickness of these eggshell fragments varies from 2.3 to 2.7 mm, with an average value of 2.54 mm and they are thicker than in the Recent *S. camelus* (eggshell thickness 1.6 to 2.1 mm). The pore openings are grouped together in shallow pits, the diameters of which vary from 0.5 to 1 mm, and their density varies from 10 to 20 per cm^2. Each pit contains about 50 pore openings. *Struthio asiaticus* was widespread during the Pliocene in Europe and Asia (Mourer-Chauviré & Geraads, 2008).

Order Procellariiformes

Family Diomedeidae

Genus *Phoebastria* Reichenbach, 1852

Although albatrosses are no longer present in the North Atlantic, they were numerous during the Pliocene whith five species known from the marine deposits of the Yorktown Formation in North Carolina, USA (Olson & Rasmussen, 2001). In the Palaearctic region, an extinct species was described from England, *Phoebastria anglica* (Lydekker, 1891). It was previously known by a tarsometatarsus and pedal phalanx from the Red Crag, Foxhall, Suffolk, and by an ulna from the Coralline Crag, Orford, Suffolk (C. Harrison & Walker, 1978). To those remains have been added a complete ulna and a partial humerus from the Nordwich Crag, Suffolk (Dyke *et al.*, 2007). These localities are dated to the upper Pliocene and are therefore contemporaneous with Ahl al Oughlam.

All of the fossil albatrosses found at Ahl al Oughlam belong to the genus *Phoebastria*, most of whose species live in the Pacific Ocean, generally North of the tropic of Cancer. The exception is *P. irrorata*, the Waved Albatross, or Galapagos Albatross, which lives in the intertropical zone of the East Pacific (del Hoyo *et al.*, 1992). It is possible that, before the closure of the Panamanian Isthmus, there were circular oceanic currents around the earth that made it easier for organisms to be dispersed between the North Pacific and the North Atlantic. We know that species of the genus *Phoebastria* survived for at least 2 Ma in the North Atlantic after the closure of the Panamanian Isthmus because Olson & Hearty (2003) showed that a breeding colony of *P. albatrus* was present on Bermuda and was probably extirpated by the sea-level rise of the Marine Isotope Stage 11 interglacial, dated at about 400,000 years ago.

With the exception of a New Zealand population of *D. epomophora*, all the Recent albatrosses breed on islands, due to avoidance of mammalian predators. The Ahl al Oughlam albatrosses could have bred in the Canary, Salvage, Madeira, or Azores archipelagoes.

Phoebastria anglica (Lydekker, 1891)

Fig. 2A

Material. Right humerus, shaft and slightly incomplete distal part, AaO-3467; left humeri, fragment of proximal part, AaO-2691, shaft, AaO-2690, distal part, AaO-714, fragment of distal part, AaO-2621; left carpometacarpi, proximal part, AaO-2622, distal part, AaO-822; right carpometacarpus, distal part, AaO-2623; right femora, proximal part with pelagornithid vertebrae, AaO-713, proximal part, AaO-2625.

This species is also known from the Bone Valley Formation, Florida, and the San Diego Formation, California, and very numerous remains have been found in the Yorktown Formation, North Carolina (Olson & Rasmussen, 2001). Among the five albatross species identified from this locality, *P. anglica* is the largest. Unfortunately the authors above do not give measurements of elements comparable to those found at Ahl al Oughlam. Published measurements of *P. anglica* are slightly smaller than those of *Diomedea exulans*, the Wandering Albatross, and very close to those of *D. amsterdamensis*, the Amsterdam Albatross. We measured five specimens of Recent *D. exulans* and a set of subfossil postcranial bones of *D. amsterdamensis* from at least two different individuals, in the USNM collection. The elements found at Ahl al Oughlam are also characterized by dimensions smaller than those of *D. exulans* and close to those of *D. amsterdamensis* (Table 1). We consider therefore it is possible to assign them to *P. anglica*.

Phoebastria sp. cf. *P. albatrus* (Pallas, 1769)

Fig. 2B–H

Material. Posterior part of cranium, AaO-2626; right quadrates, AaO-2627, 2628; right coracoid, almost complete, and right scapula, proximal part, AaO-892; right humeri, proximal part and shaft, AaO-2624, fragment of proximal part, AaO-717, and shaft possibly from the same bone, AaO-704, distal part, AaO-716, fragment of distal part, AaO-2633; left humeri, fragment of proximal part, AaO-720, distal parts, AaO-843, 4297; articulated bones including right humerus, distal part, right ulna, proximal part and shaft, right radius, proximal part and shaft, and two sesamoids, AaO-820; right radius, proximal part, AaO-418; right carpometacarpi, proximal part, juv., AaO-4796, distal parts and shaft, AaO-2629, 2630; left carpometacarpi, almost complete, AaO-4800, proximal part, AaO-845, distal part, AaO-824; phalanx 1 of right major digit of wing, AaO-2631; phalanx 1 of left major digit of wing, proximal part, AaO-823; phalanx 2 of left major digit of wing, AaO-2632; right femora, AaO-715, distal part, AaO-847; left femora, AaO-722, proximal part, AaO-846; left tibiotarsus, distal part, AaO-2634.

The Recent North Pacific albatrosses, which belong to the genus *Phoebastria* (Nunn *et al.*, 1996), have some morphological characteristics that differ from those of the genera *Diomedea, Phoebetria* and *Thalassarche*, in particular in the shape of the tarsometatarsus and in its relative length compared to the ulna (Olson & Rasmussen, 2001; Dyke *et al.*, 2007). Unfortunately the tarsometatarsi are absent from the Ahl al Oughlam material. The elements listed above have been designated as *P.* sp. cf. *P. albatrus* because they are more similar, morphologically and morphometrically to this species than to any other described taxa. Some of their dimensions, however, are slightly smaller than those of a population including recent forms and subfossil forms from middens (Table 2 and Fig. 3).

Measurements of the posterior part of cranium (AaO-2626) in mm: Greatest width of the posterior part at level of zygomatic processes: 55.6; width of the calvarium at level of temporal fossae: 44.9; least width of the frontal at level of indentation between the lacrimals and the postorbital processes: 17.5.

Measurements of the coracoid and scapula (AaO-892) in mm: (on the coracoid the ventralmost tip of the acrocoracoid

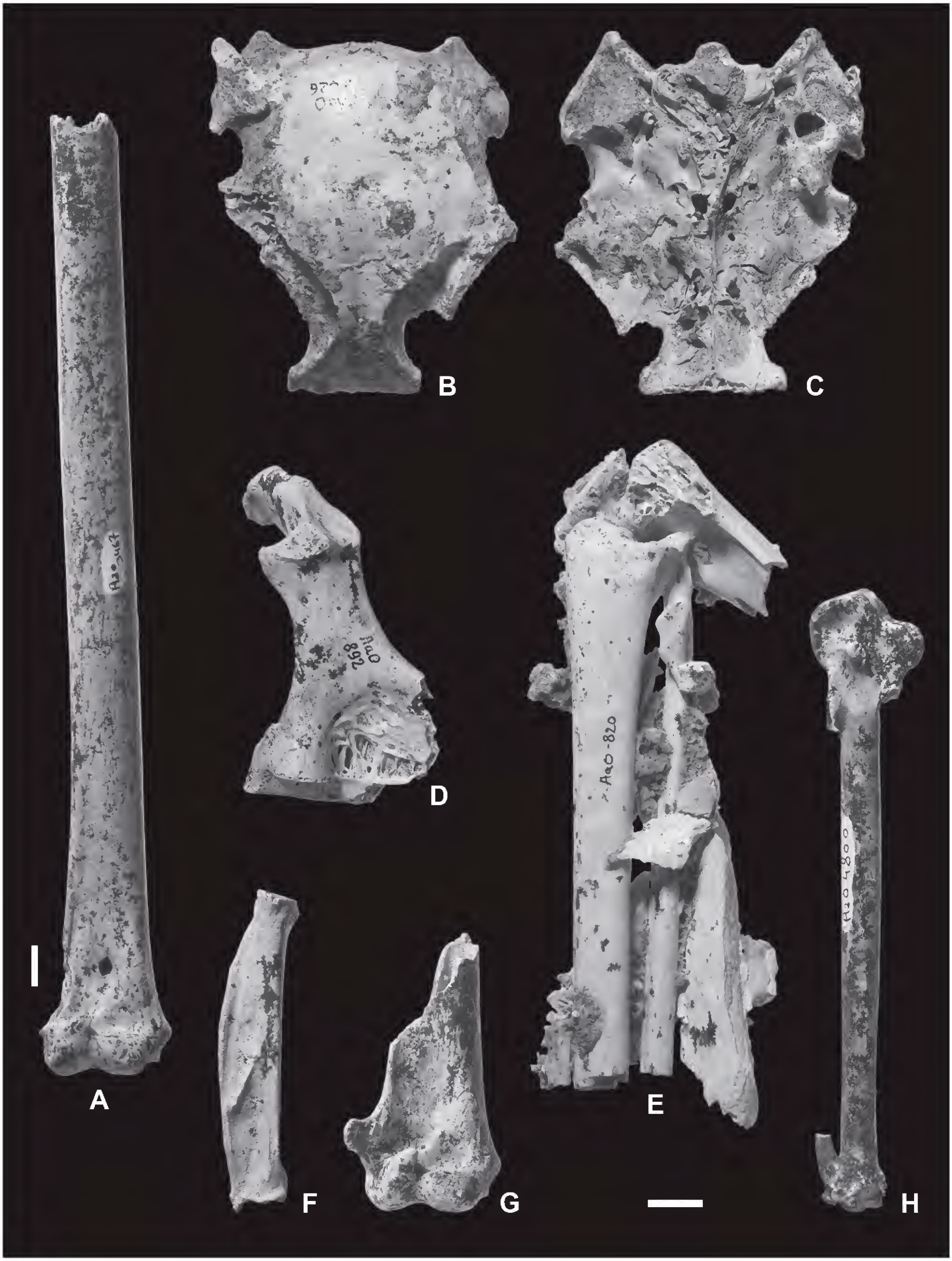

Figure 2. (*A*) *Phoebastria anglica*, right humerus, shaft and distal part, AaO-3467, cranial view. *Phoebastria* sp. cf. *P. albatrus, B–H*: (*B*) posterior part of cranium, AaO-2626, dorsal view; (*C*) idem, ventral view; (*D*) right coracoid, AaO-892, dorsal view; (*E*) right humerus, distal part, right radius and right ulna, proximal parts, articulated, and two sesamoids, AaO-820, caudal view; (*F*) phalanx 1 of right major digit of wing, AaO-2631, dorsal view; (*G*) right humerus, distal part, AaO-716, cranial view; (*H*) left carpometacarpus, AaO-4800, ventral view. The scale bars represent 1 cm. Same scale bar for *B–H*.

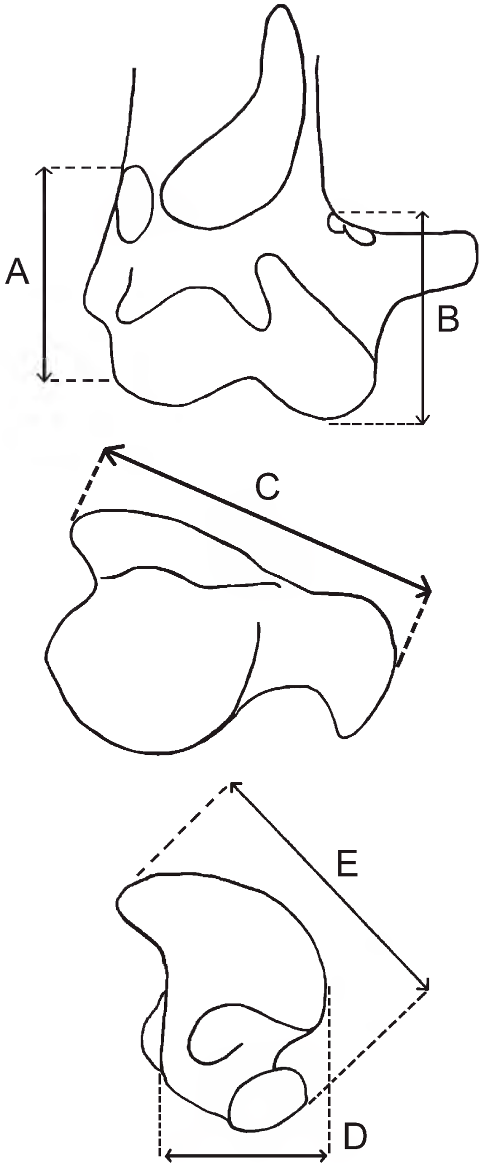

Figure 3. Diagram showing the measurements on the distal part of the humerus (*A, B*), the proximal part of the ulna (*C*), and the distal part of the carpometacarpus (*D, E*) in the genera *Phoebastria* and *Diomedea* (Tables 1 and 2).

and the tip of the procoracoid are not preserved).

Coracoid: Total length measured on the medial side, 60.2; width from the medial side of Facies scapularis to the lateral side of Facies articularis humeralis, 19.0; depth from the dorsal side of Facies scapularis to the ventral end of the acrocoracoid, ca. 30.1; width of shaft in the middle, 14.6; depth of shaft at the same level, 10.2; greatest depth of sternal facet on the medial side, 14.7.

Scapula: Proximal width from acromion to Facies articularis humeralis, 18.0.

The specimen no. AaO-820, which includes a distal humerus, a proximal ulna, and a proximal radius, all articulated, shows two sesamoids that are situated just distally compared to the place where the head of the radius comes to rest against the dorsal cotyla of the ulna. Examination of Recent skeletons of *P. albatrus* and *P. nigripes* from the USNM collection shows the occurrence, on some skeletons, of two osseous nodules, one rounded and one elongate, bound together by a supple tendon which is inserted on the dorsal side of the Processus supracondylaris dorsalis of the humerus. When the wing is flexed these two sesamoids position themselves in the space between the radius and the ulna, as in the fossil. It is possible to see these sesamoids when the skeletons still have some ligaments.

Greatest length of the elongate sesamoid on AaO-820: 17.5 mm; on a Recent *P. albatrus* (USNM 576025): 18.3 mm.

Phoebastria sp. cf. *P. nigripes* (Audubon, 1849)

Fig. 4A

Material. Left quadrate, AaO-2635; right humerus, fragment of proximal part, AaO-721; left humeri, distal parts, AaO-718, 2636; right carpometacarpus, distal part and shaft, AaO-2637; left carpometacarpus, proximal part, AaO-2692; right femur, almost complete, subadult, AaO-2638; left femur, proximal part, AaO-719.

This is the smallest of the three species of albatrosses found at Ahl al Oughlam. Its measurements correspond closely to those of the Recent *P. nigripes* (Table 2), and are larger than those of *Phoebastria* aff. *P. immutabilis*, and those of the extinct *P. rexsularum*, from the Yorktown Formation (Olson & Rasmussen, 2001).

Family Procellariidae

Genus *Calonectris* Mathews & Iredale, 1915

Calonectris sp. cf. *C. diomedea* (Scopoli, 1769)

Material. Right humerus, slightly incomplete proximal part, from a subadult individual, AaO-723; right femur, proximal part, AaO-2697.

This humerus differs from the similar-sized species of procellariid (genera *Puffinus, Pterodroma, Bulweria*) by its morphological characteristics and it is in perfect agreement with the genus *Calonectris*. In *Puffinus* the Caput humeri is more developed both in proximo-distal and craniocaudal directions and is more projecting over the Fossa tricipitalis (*sensu* Ballmann, 1969) than in *Calonectris*. The Tuberculum dorsale is proximo-distally elongate in caudal view, and is projecting proximad, whereas in *Calonectris* it is more rounded and less projecting. The Tuberculum ventrale is proportionally more developed and more caudally projecting in *Puffinus* than in *Calonectris*. In *Calonectris*, as well as in *Puffinus*, there is a small protuberance, distally directed, on the Crus dorsale of the Fossa pneumoanconaea (*sensu* Ballmann, 1969), but this protuberance is more developed in *Calonectris*. On the caudal surface, the Margo caudalis goes vertically in proximal direction, then describes a curve which joins the humeral head in *Calonectris* whereas in *Puffinus* it does not make a curve and joins the distal border of the dorsal tubercle.

The shaft of the humerus is almost circular in *Calonectris* whereas it is flattened in *Puffinus*, but unfortunately this is not visible on the fossil the shaft of which is not preserved.

In the subgenus *Thyellodroma* (species *Puffinus (Thyellodroma) pacificus*) the morphological characteristics of the proximal part of the humerus are slightly different from

Table 1. Measurements (mm) of fossil *Phoebastria anglica*, from Ahl al Oughlam, and Recent *Diomedea amsterdamensis* and *D. exulans*. Measurement A: from the proximal end of the attachment of anterior articular ligament (Howard, 1929) to a small groove situated between the processus flexorius and the condylus ventralis, on the ventral side of the distal extremity (Fig. 3). For *Diomedea exulans* the following specimens have been measured: USNM 18554, 321465, 321749, 488376, 559552. Data presented as: mean [observed range].

	Diomedea amsterdamensis Recent (n = 2)	*Diomedea exulans* Recent (n = 5)	*Phoebastria anglica* Ahl al Oughlam
Humerus			
depth of caput humeri	13.15 [12.1–14.2]	14.98 [14.0–16.0]	ca. 12.0
distal width	30.50 [29.0–32.0]	34.04 [33.3–34.7]	[30.5–32.0]
distal depth	18.80 [18.3–19.3]	21.96 [21.0–23.0]	[19.6–20.3]
measurement A	23.90 [22.8–25.0]	26.56 [25.8–27.0]	[25.5–25.5]
Carpometacarpus			
proximal width	10.40 [10.4–10.4]	11.66 [11.1–12.9]	10.40
proximal depth	24.35 [24.3–24.4]	26.26 [25.9–26.6]	ca. 23.0
width of metacarp. maj. at midpoint	8.00 [8.0–8.0]	7.76 [7.2–8.2]	7.50
depth of metacarp. maj. at midpoint	8.30 [8.0–8.6]	8.56 [8.3–9.0]	8.60
distal width	11.05 [10.7–11.4]	12.52 [12.0–13.1]	[10.2–10.2]
distal depth	16.60 [16.2–17.0]	17.64 [16.8–18.4]	[ca. 16–16.3]
Femur			
proximal width	21.20 [20.8–21.6]	22.72 [22.1–23.4]	[ca. 21.6–22.9]
proximal depth	13.40 [13.2–13.6]	15.74 [15.6–15.9]	[14.5–14.7]

those of the subgenus *Puffinus* (species *Puffinus (Puffinus) griseus*) but they are more similar to the subgenus *Puffinus* than to the genus *Calonectris*.

In the genera *Pterodroma* and *Bulweria* the ventral tubercle is more projecting ventrally and the Crista delto-pectoralis is more projecting dorsally than in the genus *Calonectris*. In *Pterodroma* the humeral head forms a well defined ledge, with a rounded lobe, above Fossa tricipitalis, and the dorsal tubercle is in the continuation of the humeral head, i.e. there is no space between the humeral head and the dorsal tubercle. Still in *Pterodroma* the Fossa pneumoanconaea has a lozengic shape, obliquely elongate both in proximodistal and dorsoventral directions, whereas in *Calonectris* this fossa is more rounded. Finally in *Pterodroma* there is no protuberance directed distally on the Crus dorsale fossa.

In the Recent species *Calonectris diomedea* there are great differences in size between the two subspecies. The largest one is *C. diomedea borealis*, which breeds on the Azores, the Canaries, the Berlengas, and Madeira (Jouanin & Mougin, 1979), and the smallest one is *C. diomedea diomedea*, which breeds on the Mediterranean islands. *Calonectris edwardsii*, which breeds on the Cape Verde islands, is now considered as a distinct species (Olson, 2008) and it is smaller than the two subspecies of *Calonectris diomedea*. By its dimensions (prox. width of humerus, from tip of tuberculum ventrale to tuberculum dorsale 17.2 mm; depth of caput humeri, 4.7 mm; proximal width of the femur, 8.6 mm; proximal depth, 4.7 mm) the Ahl al Oughlam form is closer to *C. d. diomedea*. Its dimensions also correspond to those of *C. leucomelas*, which breeds on the offshore islands of the West Pacific. It is smaller than the extinct species *Calonectris krantzi* from the Pliocene of the Yorktown Formation, North Carolina (Olson & Rasmussen, 2001).

An extinct species, *Calonectris wingatei*, has recently been described from the Middle Pleistocene of Bermuda (Olson, 2008). In this species the total length of most of the bones is similar to that of *C. diomedea diomedea*, but the femur is longer and all the long bones are more robust. In the Ahl al Oughlam material the femur is similar in size to *C. d. diomedea* and it is smaller than the femur of *C. wingatei*.

The genus *Calonectris* has been reported from the lower Pliocene of Duinefontein (age 5 Ma), in South Africa (Olson, 1985a), where it is represented by a carpometacarpus slightly larger and morphologically different from that of *Calonectris diomedea*, and *Calonectris* aff. *diomedea* is present in the deposits of Lee Creek Mine, North Carolina, probably from the Pliocene of the Yorktown Formation (Olson & Rasmussen, 2001).

Order Odontopterygiformes

Family Pelagornithidae

Genus *Pelagornis* Lartet, 1857

Pelagornis mauretanicus Mourer-Chauviré & Geraads, 2008

The Odontopterygiformes, or pseudodontorns, were giant marine birds which presented bony tooth-shaped excrescences on the jaws. These pseudoteeth are unique among birds. They had a very large wingspan, up to 5.5 to 6 m, and their skeleton was highly modified. *Pelagornis mauretanicus* was approximately the same size as *P. miocaenus*, the type species of the genus, but differed morphologically. The material from Ahl al Oughlam allowed the description of several elements of the post-cranial skeleton. The pseudodontorns were distributed on the oceans all over the world from the Late Paleocene onwards. During the Pliocene, they were still present in North America, New Zealand, Japan, and Peru. The Ahl al Oughlam form, dated from 2.5 Ma, is the most recent, accurately dated form known to date (Mourer-Chauviré & Geraads, 2008).

Table 2. Measurements (mm) of fossil *Phoebastria* sp. cf. *P. nigripes* and *P.* sp. cf. *P. albatrus*, from Ahl al Oughlam, and Recent *Phoebastria nigripes* and *P. albatrus*. Measurement A: as for Table 1. Measurement B: from the proximal part of the insertion of the processus supracondylaris dorsalis on the shaft, to the distal part of the condylus dorsalis. For the ulna, the proximal diagonal (C) is measured on the caudal face, from the ventral side of the olecranon, to the dorsal side of the cotyla dorsalis. On the carpometacarpus there is a small tubercle situated proximally to the distal articular surface, on the ventral side of the shaft. The distal width (D) is measured directly on the distal articular surface, without this tubercle (Fig. 3). Data presented as: mean (n) [observed range].

	Phoebastria nigripes	***Phoebastria* sp.**	***Phoebastria albatrus***	***Phoebastria* sp.**
		cf. *P. nigripes*		**cf. *P. albatrus***
	Recent	**Ahl al Oughlam**	**Recent + middens**	**Ahl al Oughlam**
Quadrate				
maximal height	22.68 (20) [21.4–ca. 24.5]	23.5	25.29 (8) [ca. 24–26.1]	[25.0–25.4]
Humerus				
depth of caput humeri	9.06 (18) [8.2–9.6]	9.3	11.02 (18) [10.2–11.9]	[10.3–10.6–10.7]
distal width	23.18 (18) [21.2–24.2]	[21.7–23.8]	26.59 (18) [25.6–27.8]	[25.3–25.8]
distal depth	15.17 (18) [14.0–15.7]	[15.2–15.5]	17.22 (18) [16.6–18.0]	[16.1–16.6]
measurement A	19.21 (18) [17.6–21.0]	19.6	22.22 (18) [21.3–23.2]	21.1
measurement B	17.61 (18) [16.1–19.4]	[17.2–18.2]	20.47 (18) [19.0–22.2]	[19.5–20.0–ca. 22]
Ulna				
proximal diagonal (C)	19.86 (17) [18.6–20.7]	—	22.70 (2) [22.4–23.0]	21.3
Radius				
greatest diam. of shaft at midpoint	4.78 (17) [4.4–5.3]	—	5.88 (4) [5.6–6.3]	[6.1–6.5]
depth measured perpendicularly	3.65 (17) [3.2–4.0]	—	4.55 (4) [4.4–4.7]	[4.5–4.6]
Carpometacarpus				
total length	108.63 (16) [101.5–113.7]	—	113.87 (13) [107.2–120.8]	115.7
proximal width	8.03 (16) [7.7–8.4]	7.9	9.14 (13) [8.6–9.5]	[8.7(subadult)–9.0]
proximal depth	19.88 (16) [19.0–20.7]	19.6	21.68 (13) [20.2–23.1]	[21.1(subadult)–21.4]
width metacarp. maj. at midpoint	5.30 (16) [4.9–5.6]	5.8	6.74 (13) [6.2–7.4]	[6.4–6.7–6.7]
depth metacarp. maj. at midpoint	6.38 (16) [5.8–6.9]	6.1	7.10 (13) [6.2–8.0]	[6.7–7.0–7.6]
distal width (D)	8.79 (16) [7.6–9.4]	ca. 8	10.25 (12) [9.8–10.7]	[9.2–9.2–10.2]
distal depth (E)	13.04 (16) [12.2–14.1]	—	14.47 (12) [13.7–15.3]	[13.2–13.6]
Phalanx I major wing digit				
length	53.77 (16) [50.1–57.8]	—	58.2 (1)	59.2
Femur				
total length	78.25 (18) [74.1–82.3]	ca. 79 (subadult)	89.79 (15) [86.6–94.7]	[81.7–87.0]
proximal width	15.76 (18) [15.0–17.2]	[15.5(subadult)–16.4]	18.68 (13) [17.5–19.3]	[17.6–18.3–ca. 19]
proximal depth	10.61 (18) [9.9–11.4]	[9.8–10.2 (subadult)]	12.61 (14) [12.0–13.4]	[10.4–ca. 10.5–12.3]
maximal width of shaft at midpoint	7.50 (18) [7.0–7.9]	7.7 (subadult)	8.73 (15) [8.1–9.5]	[8.2–8.7]
depth of shaft at midpoint	6.66 (18) [6.1–7.1]	7.4 (subadult)	7.73 (15) [7.3–8.5]	[8.0–8.0]
distal width	16.71 (18) [15.8–17.9]	ca. 17 (subadult)	19.60 (14) [18.7–21.3]	[17.8–19.8]
distal depth	13.17 (18) [11.8–14.0]	—	14.51 (14) [13.8–15.4]	[14.3–ca. 15]

Order Pelecaniformes

Family Sulidae

Genus *Morus* Vieillot, 1816

Morus peninsularis Brodkorb, 1955

Fig. 4B–D

Material. Right quadrates, AaO-727, 827; left quadrate, AaO-728; vertebrae, AaO-819, 828, 829, 830, 831, 832, 833, 834, 871; right coracoid, sternal part and shaft, AaO-725; left coracoid, almost complete, AaO-2108; right humerus, fragment of distal parts, AaO-730, 2639; left humerus, distal part, AaO-726; right ulna, distal part, AaO-2642; left ulna, proximal part, AaO-2641; right carpometacarpi, AaO-2643, 2644; alar phalanges, AaO-2645, 2646, 2647; left femora, AaO-724, proximal part, AaO-2648; right tibiotarsus, distal part, AaO-729; right tarsometatarsus, distal part, AaO-731, trochlea of digit IV, AaO-732.

The species *Morus peninsularis* was described by Brodkorb (1955) from the Upper Bone Valley locality, in Florida, which is dated to the lower Pliocene, age about 5 to 4.5 Ma (Becker, 1987a,b). This species is very abundant in the Pliocene Yorktown Formation, North Carolina (Olson & Rasmussen, 2001). The holotype of the species is an almost complete coracoid. Compared to the holotype, the Ahl al Oughlam coracoid AaO-2108 is of similar length but slightly more robust. The length of the dorsal and ventral sternal facets is longer, the acrocoracoid bulges a little more, and the pneumatic foramina are slightly more developed. In *Morus bassanus* the scapular facet is strongly projecting dorsally, but it is less projecting in *M. peninsularis*. Also in *M. bassanus* the clavicular facet is medioventrally oriented while in *M. peninsularis* it is more ventrally oriented. By these two characteristics the coracoid AaO-2108 is more similar to *M. peninsularis*.

The dimensions of the specimens referred to *Morus peninsularis* are similar to the dimensions of those from the Yorktown Formation preserved in the USNM collection and illustrated by Olson & Rasmussen (2001, pl. 12 and 13), except for the distal part of tibiotarsus AaO-729, which is slightly smaller (Table 3). The carpometacarpus AaO-2643 has a large pneumatic foramen on the ventral face, in the Fossa infratrochlearis, but this is not visible on the specimen AaO-2644 which is incompletely preserved. Both carpometacarpi have another, small, foramen, going right through the Processus alularis, at the level of the junction

Table 3. Measurements (mm) of fossil *Morus peninsularis* and *Morus* sp. cf. *M. bassanus*, from Ahl al Oughlam.

	Morus peninsularis			***Morus* sp. cf. *M. bassanus***		
Quadrate	AaO-727	AaO-728	AaO-827			
total length	19.3	19.8	20.8			
width at the top of proc. oticus	10.2	9.8	9.9			
max. width of proc. mandibularis	14.8	15.7	16.8			
Coracoid	AaO-2108	AaO-725				
internal length	55.3	—				
width of ventral sternal facet	17.3	—				
width of dorsal sternal facet	13.5	13.5				
length from head to procoracoid	24.7	—				
depth of head	13.6	—				
depth at level of scapular facet	19.3	—				
least depth of shaft	7.4	7.2				
Humerus	AaO-726	AaO-730		AaO-733	AaO-734	AaO-4801
depth of head	—	—		9.8	—	—
length of deltoid crest [a]	—	—		49.0	—	—
width of shaft at midpoint	—	—		10.3	—	—
depth of shaft at midpoint	—	—		9.5	—	—
distal width	20.5	—		—	ca. 23.5	23.3
distal depth	—	14.0		—	—	14.6
Ulna	AaO-2641	AaO-2642		AaO-2640		
proximal width	15.2	—		16.3		
proximal depth	—	—		16.0		
width of shaft at midpoint	—	—		9.0		
depth of shaft at midpoint	—	—		9.1		
depth of internal condyle	—	11.6				
Carpometacarpus	AaO-2643	AaO-2644		AaO-747		
total length	81.2	ca. 85		—		
proximal width	9.0	—		—		
proximal depth	17.6	—		—		
width of maj. metacarp. at midpoint	5.1	6.0		—		
depth of maj. metacarp. at midpoint	6.7	6.8		—		
distal width	ca. 8	8.0		7.9		
distal depth	11.7	12.2		12.7		
Phalanx 1 major wing digit	AaO-2645	AaO-2646	AaO-2647			
total length [b]	41.5	44.6	39.3			
Femur	AaO-724	AaO-2648		AaO-826		
total length	71.5	—		—		
proximal width	14.2	—		—		
proximal depth	11.6	10.4		—		
depth of head	7.2	—		—		
width of shaft at midpoint	ca. 7.0	6.4		7.0		
depth of shaft at midpoint	7.9	7.4		7.4		
distal width	14.8	—		16.5		
distal depth	12.8	—		12.8		
Tibiotarsus	AaO-729					
distal width	12.5					
distal depth	12.1					
Tarsometatarsus	AaO-731					
distal width	14.7					
distal depth	8.3					

[a] From the dorsal tubercle to its attachment to the shaft.

[b] Without the internal index process.

between the alular and the major metacarpals. The femora also have a pneumatic foramen on the cranial face, distal to the Crista trochanteris. These pneumatic foramina are less developed in Recent species of the genus *Morus*.

Morus sp. cf. *M. bassanus* (Linnaeus, 1758)

Fig. 4E–F

Material. Right humerus, proximal and distal parts, probably from the same bone, AaO-733, 734; right humerus, distal part, AaO-4801; left ulna, proximal part and shaft, AaO-2640; left carpometacarpus, distal part, AaO-747; right femur, distal part, AaO-826.

The dimensions of the remains referred to *Morus* sp. cf. *M. bassanus* are included in the variation range of a series of 14 Recent individuals from the USNM collection (Table 3). There is not much difference in the femur dimensions between *Morus peninsularis* and *M.* sp. cf. *M. bassanus* from Ahl al Oughlam. The main difference is in the distal width which is slightly larger in the Moroccan form. This is related to the fact that the medial condyle is more medially projecting in *Morus bassanus* than in *Morus peninsularis*.

The large forms, larger than *Morus bassanus* (*Morus*, undescribed species 1 and 2), that were present in the Yorktown Formation (Olson & Rasmussen, 2001) are not represented at Ahl al Oughlam.

Order Ciconiiformes

Family Threskiornithidae

Genus *Geronticus* Wagler, 1832

Geronticus olsoni n.sp.

Fig. 4G–K

Holotype. Left coracoid, AaO-741.

Horizon and locality. Late Pliocene, age about 2.5 Ma, Ahl al Oughlam, southeast boundary of the city of Casablanca, Morocco.

Paratypes. Left coracoid, slightly incomplete, AaO-837.

Referred material. Right humeri, distal part and shaft, AaO-838, distal parts, AaO-736, 746; left humeri, proximal part, juv., AaO-4804, distal part, AaO-739; right ulna, shaft, AaO-2649; left ulna, proximal part, AaO-4802; right radius, distal part, AaO-2650; left radii, proximal part, AaO-3099, distal part, AaO-4798; right carpometacarpi, distal parts, juv., AaO-742, 848, 2651; left carpometacarpi, distal part, AaO-737, 745, 2662, distal part, juv., AaO-738; phalanges 1 of major digit of wing, AaO-740, 743, 744; right femur, incomplete, AaO-2652; left tibiotarsi, proximal parts, AaO-825, 2653, distal part, AaO-2654; right tarsometatarsus, two trochleae, AaO-752; left tarsometatarsus, almost complete, AaO-2655.

Diagnosis. Species belonging to the genus *Geronticus* and differing from the two Recent species, *G. eremita*, the Northern Bald Ibis, and *Geronticus calvus*, the Southern Bald Ibis, and from the extinct species *G. apelex*, by its larger size.

Measurements. See Table 4.

Etymology. To Storrs L. Olson, Senior Scientist at the Smithsonian Institution in recognition of his help during the time Cécile Mourer-Chauviré spent at the USNM, in Washington, and in recognition of Helen James' and Storrs' hospitality in their home, during the same period.

Curation of the material. The material will be deposited at the Institut National des Sciences de l'Archéologie et du Patrimoine (INSAP), in Rabat, Morocco.

Description and comparisons. Detailed osteological comparisons with the genera of Threskiornithidae present in the collections of USNM, UCBL, and Institut de Paléontologie Humaine, MNHN Paris, make it possible to refer this material to the genus *Geronticus*. Generally, in the genus *Geronticus*, the medial part of the sternal facet of the coracoid forms a projecting point, and the medial side of the shaft is concave. However this feature may be subject to a certain amount of variation as in the two skeletons of *G. eremita* from UCBL, one has a much more projecting point than the other one. The same variation can be observed in Olson's paper on Pliocene ibises of South Africa (Olson, 1985b). The coracoid of *G. apelex* has a point that projects only slightly (Olson 1985b, fig. 5 A) while that of *G. calvus* has a slightly more projecting point (Olson 1985b, fig. 5B). On the two coracoids from Ahl al Oughlam the point is not very projecting and the medial side of the shaft is straighter. However despite this one difference the coracoids of Ahl al Oughlam are similar in all other characteristics to those of Recent members of the genus *Geronticus*. The procoracoid is well developed medially and extends farther mediad than the acrocoracoid; the Foramen nervi supracoracoidei is situated at a similarly great distance in the sternal direction from the scapular facet; the sternal facet is oblique compared to the longitudinal axis of the bone and the Processus lateralis extends very far in the lateral direction; on the dorsal face, on the medial side, just proximally to the sternal facet, there is a small elongate and flattened surface, along the medial border. This surface is also present in the Recent specimens of *G. eremita*.

The distal humeri also share the characteristics of the genus *Geronticus*. They are not very elongated ventrad. The ectepicondylar prominence forms a elongated proximad and projecting dorsad ridge. The attachment of the anterior articular ligament is not very raised compared to the cranial face. The impression of M. brachialis is shallow. There are no particular morphological characteristics on the ulna. A few Papillae remigales caudales are visible.

The distal part of the tibiotarsus is similar to *Geronticus* due to its strong elongation mediad, the medial condyle is much narrower than the lateral condyle and the Incisura intercondylaris is wide. The tubercle that is found on the lateral side of the distal opening of the Canalis extensorius is not strongly developed in the genus *Geronticus*, while it is much more developed in the genus *Threskiornis*. Both Tuberositates retinaculi extensoris are not strongly projecting in the genus *Geronticus*, while they are more developed in the closely related and potentially confusing genus *Pseudibis*.

The tarsometatarsus is short and robust as in the genus *Geronticus*. The Sulcus extensorius is deep proximally, and edged by two ridges. The hypotarsus presents two main ridges. The Crista medialis hypotarsi is incompletely preserved but the Crista lateralis is preserved and has a flattened plantar surface. The two ridges are separated by an open groove. The hypotarsus does not project far plantarly. It is separated from the Cotylae lateralis and medialis by a flattened Sulcus ligamentosus. The Cotyla lateralis has a rounded outline. On the plantar face, the Fossa parahypotarsalis medialis is deep. The lateral face of the shaft is much thicker than the medial face. The Fossa metatarsi I is situated entirely on the plantar face. The opening of the Foramen vasculare distale, on the plantar side, is situated just proximally to the Incisura intertrochlearis lateralis. In all these characteristics the Ahl al Oughlam tarsometatarsus fits the genus *Geronticus*. It differs from members of the genus *Pseudibis* which have a Cotyla lateralis with a proximally projecting tubercle in the latero-plantar corner, giving a subquadrangular shape, where the canal which separates the two hypotarsal ridges is roofed, and where the plantar opening of the Foramen vasculare distale is situated further proximally compared to the Incisura intertrochlearis lateralis.

Geronticus olsoni is, on average, 13% larger than the mean of two specimens of Recent *G. eremita*. According to the measurements given by Olson (1985b) for the main long bones of the two Recent species of bald ibises, the coracoid has the same size, but the wing bones (humerus, ulna, carpometacarpus) are distinctly shorter, the tarsometatarsus is slightly shorter, and the femur is slightly longer in *G. calvus* than in *G. eremita*. Using the measurements given by Olson (1985b) the main long bones of *G. olsoni* are, on average, 12% larger than those of Recent *G. eremita* (n = 4) and 16% larger than those of *G. calvus* (n = 3). The only extinct species described so far in the genus *Geronticus* is *G. apelex* from the lower Pliocene of Langebaanweg, in South Africa (Olson, 1985b). On average *G. olsoni* is 28% larger

Table 4. Measurements (mm) of fossil *Geronticus olsoni* n.sp., from Ahl al Oughlam, fossil *Geronticus apelex*, from Langebaanweg, and Recent *Geronticus eremita*.

	Geronticus olsoni n.sp. Ahl al Oughlam		*Geronticus* *eremita*	*Geronticus* *apelex*
Coracoid	Holotype AaO-741	Paratype AaO-837	Recent mean (n = 2)	(Olson, 1985b)
internal length	53.0	52.4	46.55	40.4
width pars omalis [a]	14.8	—	14.10	—
depth pars omalis	13.0	12.7	12.00	—
length sternal part [b]	29.2	—	26.85	—
length sternal facet	24.7	ca. 21.3	22.55	—
depth sternal facet	6.6	6.0	4.35	—
width of shaft at midpoint	10.9	9.6	9.10	—
depth of shaft at midpoint	7.4	7.6	6.55	—
Humerus	mean (n)			
total length	est. 145 (1)		127.20	111.4
distal width	24.05 (4)		21.10	ca. 18.5
distal depth	13.07 (3)		11.30	—
width of shaft at midpoint	10.7 (1)		9.10	—
depth of shaft at midpoint	8.9 (1)		7.75	—
Ulna				
total length	est. 160 (1)		138.25	122.5
proximal width	ca. 14.5 (1)		13.60	13.3
width of shaft at midpoint	7.2 (1)		6.55	5.5
depth of shaft at midpoint	7.4 (1)		7.00	6.1
Radius				
greatest prox. diameter	8. 1 (1)		7.70	6.7
distal width	10.45 (2)		9.60	8.9
greatest diameter of shaft at midpoint	5.1 (1)		4.55	4.6
least diameter of shaft at midpoint	4.2 (1)		3.30	3.2
Carpometacarpus				
total length	est. 87 (1)		70.65	60.8
distal width	7.35 (4)		7.20	—
distal depth	11.65 (4)		10.70	9.2
width metacarp. maj. at midpoint	6.08 (6)		5.40	5.0
depth metacarp. maj. at midpoint	4.68 (6)		4.35	3.9
Phalanx 1 major wing digit				
length [c]	32.8 (3)		31.35	—
Femur				
total length	ca. 68 (1)		65.15	57.4
width of shaft at midpoint	6.9 (1)		6.35	5.5
depth of shaft at midpoint	7.0 (1)		5.90	4.9
Tibiotarsus				
total length [d]	129.0 (1)		113.80	—
proximal width	14.3 (2)		12.40	10.1
proximal depth	ca. 18.4 (1)		15.85	—
distal width	13.7 (1)		10.85	—
distal depth	14.0 (1)		11.45	—
width of shaft at midpoint	7.4 (1)		6.00	5.2
depth of shaft at midpoint	6.0 (1)		5.50	4.3
Tarsometatarsus				
total length	80.5 (1)		71.80	64.6
proximal width	15.2 (1)		13.20	11.6
proximal depth	ca. 14.0 (1)		12.00	10.9
width trochlea III	5.4 (1)		5.10	4.5
depth trochlea III	8.1 (1)		6.55	5.9
width of shaft at midpoint	7.0 (1)		5.30	4.9
medial depth of shaft at midpoint	4.4 (1)		3.70	—
lateral depth of shaft at midpoint	5.1 (1)		4.75	3.8

[a] From the glenoid facet to the procoracoid.

[b] From the angulus medialis to the processus lateralis.

[c] Without the internal index process.

[d] Without the cnemial crests.

than *G. apelex*.

The area of Casablanca where Ahl al Oughlam is situated is close to the region where *Geronticus eremita*, an endangered species (del Hoyo *et al*., 1992), is still breeding. At the present time the Northern Bald Ibis nests on cliff ledges and among boulders on steep slopes, by the sea or inland (Cramp & Simmons, 1977). Although there are no immature elements, it is likely that *G. olsoni* also nested in the Ahl al Oughlam area.

Order Anseriformes

Family Anatidae

Subfamily Anserinae

Anserini indeterminate

Material. Left carpometacarpus, proximal part, AaO-2663; left phalanx 1 of major digit of wing, AaO-735 (it is not possible to know whether they come from the same individual).

The carpometacarpus shows the morphological characteristics of the Anserini (Woolfenden, 1961) and its size corresponds to the Recent species *Branta canadensis*, the Canada Goose. Its measurements are (in mm): proximal width, 9.1; proximal depth, 20.8. It is larger than the extinct species *Branta woolfendeni*, from the upper Miocene or lower Pliocene of Big Sandy Fm. (Bickart, 1990).

On the phalanx the distal portion of the Pila cranialis phalangis is incomplete, mainly on the ventral side. This phalanx differs from that of the Anatinae by its much deeper Fossa ventralis. This Fossa ventralis is more developed in the proximal part of the phalanx. The measurements are (in mm): length (without the distal point), 32.4; proximal width (dorsoventrally), 8.0; proximal depth (craniocaudally), 7.3; maximum depth (craniocaudally) 10.4. As for the carpometacarpus, this phalanx is similar to that of the genus *Branta* but it is larger than the Recent *Branta bernicla*. Anserini (genus and species indeterminate) are present in the Pliocene of the Yorktown Formation. They are also comparable in size to *Branta canadensis* (Olson & Rasmussen, 2001).

Subfamily Anatinae

Genus *Alopochen* Stejneger, 1885

Alopochen sp. cf. *A. aegyptiacus* (Linnaeus, 1766)

Material. Right femur, proximal part, AaO-2660.

The proximal part of the Crista trochanteris is broken. This femur is similar to the genus *Alopochen* because the proximal part is mediolaterally compressed. The head is very globular and clearly raised compared to the proximal articular surface, but not very medially projecting. The neck is not very marked. There is a Linea intermuscularis cranialis that runs along the medial border of the proximal cranial surface.

The measurements are (in mm): proximal width (including head), 17.1; proximal depth, 12.4. They are included in the variation range of 10 Recent specimens of *A. aegyptiacus* from the USNM collection, the measurements of which are: proximal width, 14.9–20.6 (mean 17.31); proximal depth, 11.0–13.7 (mean 12.01).

This femur shows a deposit of medullary bone, which indicates that it belonged to a female and that this female died during the breeding season (Rick, 1975). At the present time, the Egyptian Goose is only found in Sub-Saharan Africa and in the central part of the Nile valley but formerly it was also present throughout the Nile valley, the Middle East and Southern Europe (Brown *et al*., 1982; del Hoyo *et al*., 1992). According to Cramp & Simmons (1977) it used to breed in Algeria and Tunisia.

Genus *Tadorna* Oken, 1817

Tadorna tadorna (Linnaeus, 1758)

Material. Right humeri, shaft and distal part, AaO-748, distal part, AaO-751; left carpometacarpus, almost complete, AaO-2658 (the alular metacarpal is missing).

Measurements. See Table 5.

The measurements of the distal humeri have been compared with those of the other species of the genus *Tadorna* from the USNM collection. They are smaller than those of *T. ferruginea, T. variegata, T. tadornoides, T. cana*, and larger than those of *T. radjah*. They are included in the variation range of the Recent *T. tadorna*, the Common Shelduck.

At the present time, the Common Shelduck breeds in Central Asia and on the European coasts, and winters in Southern China, Pakistan, India, Iran, Afghanistan, on the European Atlantic and Mediterranean coasts, and in North Africa. It still winters in Morocco (del Hoyo *et al*., 1992).

The Common Shelduck has been recorded from the Early Pleistocene, at Ubeidiya', in Israel (1.4 Ma), and Betfia, in Romania (1 Ma) (Tyrberg, 1998).

Tadorna sp.

Material. Right humerus, distal part, AaO-2656; left ulna, shaft and distal part, AaO-2657; right radii, proximal part, AaO-749, distal part, AaO-750.

Measurements. See Table 5.

The humerus no. AaO-2656 is larger than those referred to *T. tadorna*. It was compared with *Alopochen*, but *Alopochen* differs in the following characteristics: the distal part of the humerus is more elongated ventrad, the impression of M. brachialis is situated farther from the attachment of the anterior articular ligament, the ventral epicondyle is more projecting both caudally and distally. It was also compared with *Sarkidiornis melanotos*. In *Sarkidiornis*, as in *Alopochen*, the distal part of the humerus is more elongated ventrad than in the Ahl al Oughlam specimen. In *Sarkidiornis*, the impression of M. brachialis is small and situated more proximally. In particular, it is situated far from the attachment of the anterior articular ligament, whereas in AaO-2656 humerus it is just proximal to the attachment. In *Sarkidiornis*, the attachment of the anterior articular ligament is tilted and projecting cranially, while in the Ahl al Oughlam fossil it is less projecting and less tilted. The morphological characteristics of the fossil correspond to the genus *Tadorna*. By its dimensions, it is situated at the upper limit of the Recent *T. tadorna* and in the variation range of the Recent *T. ferruginea*, the Ruddy Shelduck. The measurements of

Table 5. Measurements (mm) of fossil *Tadorna tadorna* and *Tadorna* sp. from Ahl al Oughlam, and Recent *T. tadorna* and *T. ferruginea*. The measurements with an asterisk are taken from Woelfle (1967). The others were taken on specimens from the USNM collection.

	Tadorna tadorna Ahl al Oughlam		***Tadorna tadorna*** Recent	
			observed range	mean (n)
Humerus	AaO-748	AaO-751		
distal width	15.5	15.6	13.6–17.5	15.93 (9)
distal depth	9.4	9.3	9.1–10.7	9.97 (9)
width of shaft at midpoint	8.0	—	—	—
depth of shaft at midpoint	6.7	—	—	—
Carpometacarpus	AaO-2658			
total length	60.8		52.7–67.0*	61.40 (16)*
proximal width	6.5		—	—
width of metacarp. maj. at midpoint	5.5		—	—
depth of metacarp. maj. at midpoint	4.6		—	—
distal width	5.4		—	—
distal diagonal	8.3		7.3–9.2*	7.97 (16)*
	***Tadorna* sp.**			
Ulna	AaO-2657			
distal diagonal	11.6		10.5–12.8*	11.47 (20)*
depth of condylus dorsalis	10.0		—	—
with of shaft at midpoint	5.7		—	—
depth of shaft at midpoint	5.7		—	—
	***Tadorna* sp.**			
Radius	AaO-749	AaO-750		
greatest proximal diameter	6.2	—	5.5–7.0*	6.26 (21)*
greatest diameter of shaft at midpoint	3.7	—	—	—
least diameter of shaft at midpoint	3.2	—	—	—
distal width	—	7.6	5.7–7.7*	7.14 (21)*
distal depth	—	4.1	—	—
	***Tadorna* sp.** **Ahl al Oughlam**		***Tadorna ferruginea*** Recent	
Humerus	AaO-2656		observed range	mean (n)
distal width	17.2		16.7–18.2	17.58 (5)
distal depth	10.7		10.1–11.1	10.56 (5)

the other fragments of ulna and radius are included in the variation range of both *T. tadorna* and *T. ferruginea*.

At the present time the Ruddy Shelduck is a breeding resident and non-breeding Palaearctic migrant to North Africa and Western Sahara. It was formerly common and widespread, but it is now extinct as a breeding species in many regions (Brown *et al.*, 1982).

The Ruddy Shelduck has been recorded as fossil in the lower Pleistocene of Dursunlu, in Turkey, in a layer dating from 0.9 to 1 Ma (Louchart *et al.*, 1998), and an indetermined Tadornini has been reported in the site of Gomboré II, at Melka Kunturé, Ethiopia, dated at about 0.8 Ma (Pichon, 1979).

Genus *Mergus* Linnaeus, 1758

Mergus sp.

Material. Right carpometacarpus, proximal part, AaO-2659.

This carpometacarpus has been compared with the following genera of Oxyurinae (Worthy & Lee, 2008) (*Biziura, Heteronetta, Thalassornis, Stictonetta, Malacorhynchus*) and Anatinae (*Alopochen, Tadorna, Plectropterus, Cairina, Sarkidiornis, Nettapus, Aix, Chenonetta, Amazonetta, Merganetta, Anas, Marmaronetta, Netta, Aythya, Somateria, Polysticta, Histrionicus, Clangula, Melanitta, Bucephala, Mergus*) present in the USNM collection, and it is most similar to the genus *Mergus*. The alular metacarpal is not very projecting, both cranially and proximally. The dorsal face of this alular metacarpal has a depression that is more marked in the genus *Mergus* than in the other members of Anatinae. Its proximal craniocaudal depth, 10.9 mm, is included in the variation range of the Recent species *Mergus serrator*, the Red-breasted Merganser (Woelfle, 1967).

At the present time the Red-breasted Merganser does not winter on the Atlantic coasts of Morocco, but it is present, at the same latitude, on the Atlantic coasts of North America (del Hoyo *et al.*, 1992). *Mergus* aff. *M. serrator* is also present in the Pliocene of the Yorktown Formation (Olson & Rasmussen, 2001).

Order Galliformes

Family Phasianidae

Genus *Plioperdix* Kretzoi, 1955

Plioperdix africana n.sp.

Fig. 4M–U

Holotype. Complete right humerus AaO-755.

Horizon and locality. Late Pliocene, age about 2.5 Ma, Ahl al Oughlam, southeast boundary of the city of Casablanca, Morocco.

Paratypes. Right humeri, almost complete, AaO-753, shaft, AaO-2687, distal parts, AaO-761, 769, 857; left humeri, distal parts, AaO-760, 762, 763, 4809.

Referred material. Left coracoids, almost complete,

Table 6. Measurements (mm) of *Plioperdix africana* n.sp. from Ahl al Oughlam, and *Plioperdix ponticus* from Ukraine, Moldova, and Central Asia (Bocheński & Kurochkin, 1987; Zelenkov & Kurochkin, 2009).

	***Plioperdix africana* n.sp.** Ahl al Oughlam		***Plioperdix ponticus***	
Coracoid	AaO-754	AaO-2688	observed range	mean (n)
internal length	est. 31	—	—	—
width of facies artic. humer.	3.4	3.4	—	—
greatest width at midpoint	3.3	3.3	—	—
depth at midpoint	2.2	2.2	—	—
width of sternal facet	9.1	—	6.1–6.1	6.10 (2)
length of sternal facet	7.0	—	—	—
depth of sternal part	2.9	—	—	—
Humerus	observed range	mean (n)		
total length	43.7–44.2	43.95 (2)	—	—
proximal width	11.0–11.6	11.30 (2)	—	—
depth of head	4.8–5.0	4.90 (2)	—	—
with of shaft at midpoint	3.7–4.0	3.90 (4)	—	—
depth of shaft at midpoint	2.8–3.2	3.05 (4)	—	—
distal width	7.5–8.1	7.89 (8)	6.9–7.1	6.95 (4)
distal depth	4.3–4.8	4.63 (6)	3.8–4.2	3.92 (5)
Ulna	AaO-4810			
proximal width	5.0			
Radius	AaO-2689			
total length	36.2		—	—
greatest diam. of shaft at midpoint	1.7		—	—
least diam. of shaft at midpoint	1.5		—	—
Carpometacarpus	observed range	mean (n)		
total length	22.5–23.8	23.23 (3)	20.9–21.5	21.2 (2)
proximal width	2.8–3.1	2.97 (6)	2.3–2.6	2.48 (5)
proximal depth	5.7–6.2	5.97 (3)	5.6–5.7	5.65 (2)
length of distal symphysis	3.8–4.1	3.95 (2)	—	—
width of metacarp. maj. at midpoint	2.2–2.3	2.28 (4)	—	2.1 (1)
depth of metacarp. maj. at midpoint	1.9–2.1	2.05 (4)	—	—
Tibiotarsus	AaO-764			
distal width	5.7		4.4–5.0	4.65 (6)
distal depth	5.6		—	5.0 (1)
Tarsometatarsus	AaO-856			
total length	34.9		—	28.4 (1)
proximal width	7.2		—	5.2 (1)
proximal depth	7.0		—	—
depth of medial cotyla	4.3		—	2.5 (1)
depth of lateral cotyla	3.4		2.4–2.4	2.40 (2)
distal width	6.5		5.2–5.5	5.33 (3)
width trochlea met. III	2.8		2.0–2.3	2.12 (6)
depth trochlea met. III	3.9		2.4–2.7	ca. 2.53 (6)
distance foramen to distal end [a]	6.0		3.3–5.1	4.17 (6)
smallest width of shaft	3.2		2.3–2.3	2.30 (4)
least depth of shaft	2.1		1.4–1.6	1.48 (5)

[a] Distance from the distal vascular foramen to the distal end of trochlea metatarsi III.

AaO-754, omal part, AaO-2688, shaft, subadult, AaO-757; left ulna, proximal part, AaO-4810; radius, almost complete, AaO-2689; right carpometacarpi, almost complete, AaO-756, 758, 858; left carpometacarpi, proximal part, AaO-759, proximal part and shaft, AaO-4811; right tibiotarsus, distal part, AaO-764; right tarsometatarsus, AaO-856.

Diagnosis. Species showing the morphological characteristics of the genus *Plioperdix* but larger than the only species known so far, *Plioperdix ponticus* (Tugarinov, 1940), from the Pliocene of Europe and Central Asia.

Measurements. See Table 6.

Etymology. *africana*, for Africa, because the only other species of this genus, *Plioperdix ponticus*, was described from Eastern Europe and Asia.

Curation of the material. The material will be deposited at the Institut National des Sciences de l'Archéologie et du Patrimoine (INSAP), in Rabat, Morocco.

Description and comparisons. This small galliform from Ahl al Oughlam has been compared with all the Recent African genera present in the USNM collection but it cannot be referred to any of them

The humeri have a double pneumotricipital fossa. The Fossa pneumoanconaea is widely open and penetrates up to the proximal end of the bone, under the humeral head. The Fossa tricipitalis penetrates only 1 to 2 mm under the humeral head. The tricipital fossa is continued on the caudal face of the shaft by a shallow groove, that goes distally and obliquely onto the ventral border of the shaft. This groove is very elongated distally. It is bordered on the dorsal side by a ridge, the Margo caudalis, which keeps to the Eminentia musculi latissimi dorsi posterioris (Ballmann, 1969). On the cranial side, the Sulcus transversus is very shallow and indistinctly outlined proximally.

In their description of the material referred to the genus *Plioperdix* Bocheński and Kurochkin (1987) gave three morphological characteristics for the humerus. One was this groove. Another was that the distal part of the Crista

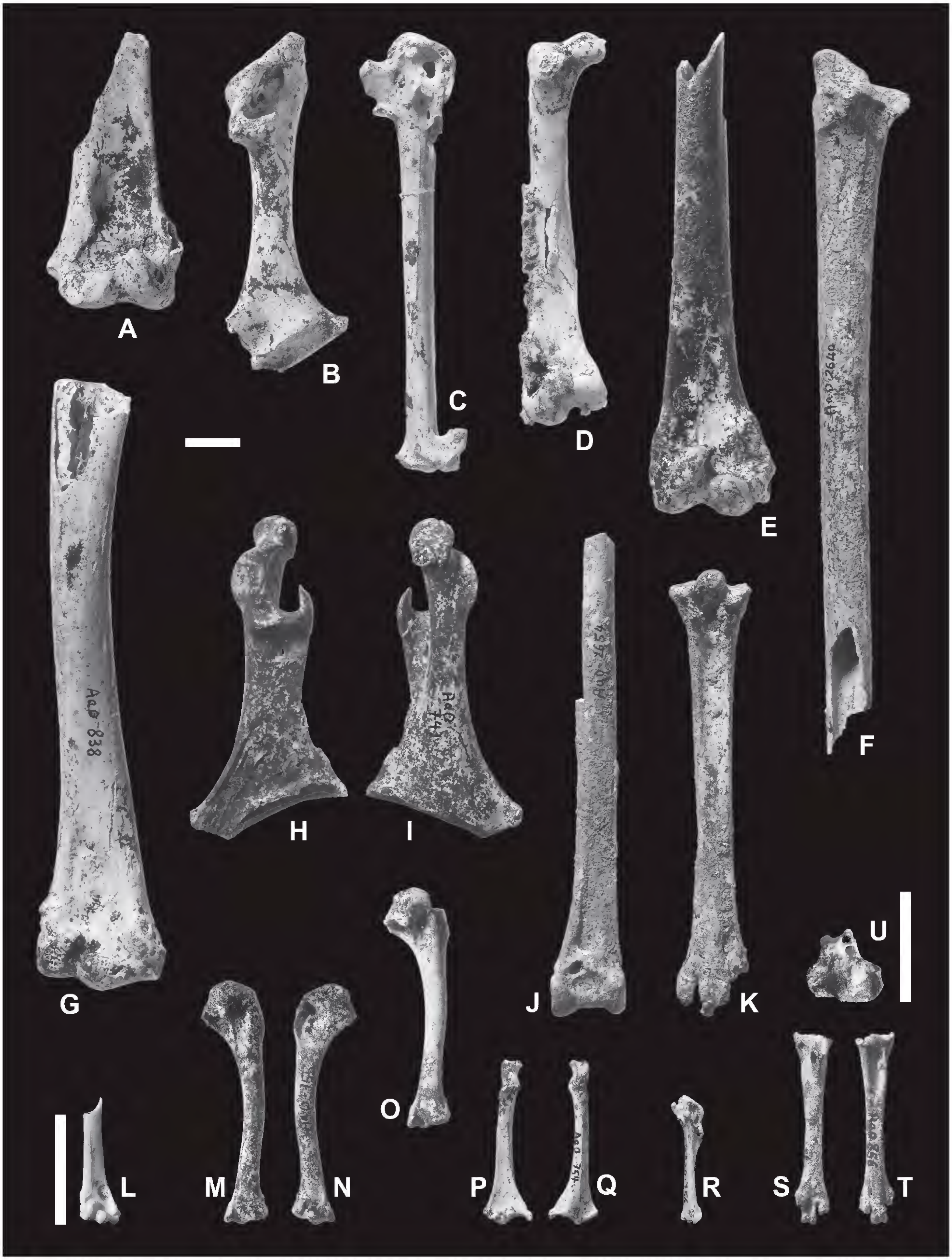

Figure 4. (*A*) *Phoebastria* sp. cf. *P. nigripes*, left humerus, distal part, AaO-718, cranial view. *Morus peninsularis*, *B–D*: (*B*) left coracoid, AaO-2108, ventral view; (*C*) right carpometacarpus, AaO-2643, ventral view; (*D*) left femur, AaO-724, caudal view. *Morus* sp. cf. *M. bassanus*, *E–F*: (*E*) right humerus, distal part, AaO-4801, cranial view; (*F*) left ulna, proximal part and shaft, AaO-2640, craniodorsal view. *Geronticus olsoni* n.sp., *G–K*: (*G*) right humerus, distal part and shaft, AaO-838, cranial view; (*H*) left coracoid, AaO-741, holotype, dorsal view; (*I*) idem, ventral view; (*J*) left tibiotarsus, distal part, AaO-2654, cranial view; … [caption continued on facing page]

pectoralis humeri ends with a sharp step. This is not very visible on the Ahl al Oughlam humeri but it is similar to what can be seen on the cranial face of the humerus of *P. ponticus* illustrated by them (Bocheński & Kurochkin, 1987, pl. XVIII, fig. 11–12). The third feature was that the Epicondylus ventralis is sharpened distally, which is also the case on the Ahl al Oughlam humeri.

The Ahl al Oughlam humeri have been compared with the humeri of the genus *Palaeortyx*. This genus is known in many European localities, from the beginning of the Late Oligocene and generally to the Middle Miocene (Göhlich & Mourer-Chauviré, 2005), but also in the Late Miocene of Hungary (Janossy, 1976), Spain (Villalta, 1963; Cheneval & Adrover, 1993), and is present until the Early Pliocene in Gargano, in Southern Italy (Ballmann, 1973, 1976; Göhlich & Pavia, 2008). A form referred to the genus *Palaeortyx* is also present in southwestern Africa, in the lower Miocene of Elisabethfeld and in the middle Miocene of Arrisdrift, both in Namibia (Mourer-Chauviré, 2003; 2008). *Palaeortyx* differs from the Ahl al Oughlam form in that the Fossa tricipitalis penetrates very deeply under the humeral head, to the end of the bone, and consequently the Fossa pneumoanconaea penetrates less deeply than the tricipital fossa. In addition the tricipital fossa continues in the disto-ventral direction as a groove which is more oblique and shorter than in the genus *Plioperdix*.

Two other genera of small galliforms, *Palaeocryptonyx* and *Chauvireria*, are present in the European Pliocene. The Ahl al Oughlam humeri have been compared with those of the type-species of *Palaeocryptonyx, P. donnezani*, from the lower Pliocene of Perpignan (MN 15) (Depéret, 1892, 1897). On the humerus of *P. donnezani*, the tricipital fossa penetrates under the humeral head, but not deeply, and is not continued as a groove crossing the shaft obliquely, in the disto-ventral direction. The humerus of *P. donnezani* is smaller than that of *P. africana*, but its deltopectoral crest is proportionally longer. The pneumatic foramen situated in the Fossa pneumoanconaea is smaller in *P. donnezani*. In *P. africana*, the distal part of the humerus is more elongate ventrad and the ventral epicondyle projects more ventrad than in *P. donnezani*.

In *Chauvireria balcanica* Boev, 1997, from the upper Pliocene of Varshets (MN 17), Bulgaria, the humerus is straighter, whereas in *P. africana* both proximal and distal parts are ventrally incurved. In *Chauvireria*, the tricipital fossa penetrates deeply under the humeral head, but it is not prolonged as a groove. The humeral head is more swollen in the proximo-distal direction than in the genera *Plioperdix* and *Palaeocryptonyx*, and the distal part is relatively narrower than in the other two genera.

The genus *Plioperdix*, with the species *P. ponticus* (Tugarinov, 1940), has been reported in the Early Pliocene of Ukraine and Moldova, and in the Late Pliocene of Transbaikalia and northern Mongolia (Bocheński & Kurochkin, 1987; Zelenkov & Kurochkin 2009). A phasianid similar to *Plioperdix ponticus* has also been reported in the Late Miocene of Southern European Russia (Titov *et al.*, 2006). Mlíkovský (1995) placed *Francolinus minor* Janossy, 1974, in synonymy with *Plioperdix ponticus* (Tugarinov, 1940), and reported this species in the locality of Stránská Skála, Musil's Talus Cone, in the Czech Republic, dated from the Early Middle Pleistocene (Tyrberg, 1998). But subsequently Mlíkovský (2002) placed the genus *Plioperdix* in synonymy with the Recent genus *Alectoris*, and the species *Plioperdix ponticus* in synonymy with *Alectoris donnezani* (Depéret, 1892). The species *donnezani* is the type-species of the genus *Palaeocryptonyx* and we have shown above that the genus *Plioperdix* differs from the genus *Palaeocryptonyx*. Therefore the occurrence of the species *Plioperdix ponticus* in the Early Middle Pleistocene relies on the correction refused of *F. minor* Janossy, 1974 to *Plioperdix* and so cannot be confirmed.

The carpometacarpi of *P. ponticus* are characterized by a Processus intermetacarpalis weakly developed, and a minor metacarpal narrow, not projecting caudally as angle, and not extending distally beyond level of Facies articularis digitalis major. Distinct fossae are located at base and in distal part of the minor metacarpal, one fossa on each side (Bocheński & Kurochkin, 1987; Zelenkov & Kurochkin, 2009). In *P. africana* the carpometacarpus is relatively shorter than in *P. ponticus*. The Processus intermetacarpalis is small and is situated very close to the proximal symphysis of the major and minor metacarpals, but it is relatively more developed than in *P. ponticus*. The minor metacarpal is only preserved on one specimen and it is very thin. The fossa which is situated on the ventral side of the distal symphysis of *P. ponticus* (Zelenkov & Kurochkin, 2009, pl. 9, figs 7b and 10b) is absent in *P. africana*.

In *P. africana*, the carpometacarpus differs from that of *Palaeortyx* because the Processus pisiformis is globular and does not extend cranially, and the Depressio muscularis interna (*sensu* Ballmann, 1969) is shallow, unlike that in the genus *Palaeortyx* (see Mourer-Chauviré *et al.*, 2004, pl. 1, fig. 5). It differs from the genus *Palaeocryptonyx* as in this genus the Processus intermetacarpalis is situated farther from the proximal synostosis of the two metacarpals. *Chauvireria* is distinguished from *P. africana* by a very robust major metacarpal, and its minor metacarpal is more robust and more distant from the major metacarpal. In *Chauvireria* the Processus intermetacarpalis is well developed, the minor metacarpal protrudes very slightly distally beyond the level of the facies articularis digitalis major, and there is a fossa on the ventral side of the distal symphysis.

Bocheński & Kurochkin (1987) then Zelenkov & Kurochkin (2009) give the morphological characteristics of the coracoid of *Plioperdix*. In *P. africana* the Pars omalis of the coracoids is incomplete but the coracoid AaO-754 agrees with *P. ponticus* in having a sternal facet very short and very curved and it lacks a pneumatic foramen in the Impressio m. sternocoracoidei. Coracoids of *Palaeocryptonyx* have a longer and less curved sternal facet and the Angulus medialis projects less mediad. AaO-754 differs also from the genus

Figure 4 [caption continued from facing page]... (*K*) left tarsometatarsus, AaO-2655, cranial view. (*L*) Rallinae, right humerus, distal part, AaO-765, cranial view. *Plioperdix africana* n.sp., *M–U*: (*M*) right humerus, AaO-755, holotype, caudal view; (*N*) idem, cranial view; (*O*) right humerus, AaO-753, paratype, caudal view; (*P*) left coracoid, AaO-754, dorsal view; (*Q*) idem, ventral view; (*R*) right carpometacarpus, AaO-756, ventral view; (*S*) right tarsometatarsus, AaO-856, plantar view; (*T*) idem, dorsal view; (*U*) idem, proximal view. The scale bars represent 1 cm. Same scale bar for *A–K* and *M–T*.

Table 7. Measurements (mm) of fossil *Otis* sp., size *Otis tarda*, from Ahl al Oughlam and Recent *Otis tarda*.

Ulna		***Otis* sp.** **Ahl al Oughlam**	***Otis tarda*** **Recent** males	 females
		AaO-766		
proximal width	observed range	24.1	23.2–25.9	17.2–18.6
	mean (n)		24.47 (3)	18.00 (4)
proximal depth	observed range	22.0	21.8–24.4	17.0–18.0
	mean (n)		23.33 (3)	17.38 (4)
		AaO-767		
depth of condylus dorsalis	observed range	17.4	18.3–19.6	14.0–14.4
	mean (n)		18.77 (3)	14.20 (2)
distal depth [a]	observed range	ca. 16.5	17.6–20.8	14.2–15.7
	mean (n)		19.10 (3)	14.95 (2)

[a] From the tuberculum carpale to the dorsal side of the condylus dorsalis.

Chauvireria, the sternal facet of which is also longer and less curved, but the Angulus medialis more projecting. In these two genera, there is no pneumatic foramen in the Impressio m. sternocoracoidei. On the ventral face, the Ahl al Oughlam coracoid shows a strong longitudinal ridge which causes a bulge of the sternal facet, while in *Palaeocryptonyx* and *Chauvireria* the sternal part is flatter.

The tarsometatarsus AaO-856 shows the principal characteristic of the genus *Plioperdix*: the trochleae are constricted rather than splayed, causing a relatively narrow distal end. Trochlea met. II is strongly pushed back plantarly and both Trochleae met. II and IV do not project significantly on the medial and lateral sides. This tarsometatarsus is subadult. The Sulcus extensorius is very deep at its proximal part. The two proximal vascular foramina are situated at the bottom of a fossa. The medial border of the Cotyla medialis projects significantly proximad as can be seen also in *Plioperdix ponticus* (see Bocheński & Kurochkin, 1987, pl. XVIII, fig. 3–4). In the two specimens of *P. ponticus* the hypotarsus is not completely preserved. There are two ridges, a medial one, and a lateral one, separated by a canal. On the Ahl al Oughlam specimen there is a roofed canal, situated approximately in the sagittal plane, and another roofed canal, narrower, situated plantarly compared to the first one. Both canals open distally by a single orifice, situated on the medial side of the hypotarsus. On the plantar face of the hypotarsus there are two smooth ridges, separated by a shallow groove. The hypotarsus is prolonged, along the plantar face, by a short median ridge. On each side of the hypotarsus there are the Fossae parahypotarsales medialis and lateralis. The Fossa parahypotarsalis lateralis is bordered by a ridge on its lateral side. The Fossa met. I is hardly visible. As Bocheński & Kurochkin (1987) have indicated, the tarsometatarsus of *Plioperdix* is very different from that of *Ammoperdix*. The most striking characteristic of the *P. africana* tarsometatarsus is that its distal width is less than its proximal width.

The measurements of *P. africana* are given in Table 6. On average, the dimensions of *P. africana* are 30% larger than those of *P. ponticus*.

Order Gruiformes

Family Rallidae

Rallinae size *Porzana pusilla* (Pallas, 1776)

Fig. 4L

Material. Right humerus, distal part, AaO-765.

Among all the Recent genera with which it was compared, it looks most similar to the genus *Porzana*. It differs from *Porzana*, however, by the strong deepening of its Fossa m. brachialis. Its distal width is 3.7 mm. In one Recent *Porzana pusilla* the distal width is also 3.7 mm.

Family Otididae

Genus *Otis* Linnaeus, 1758

Otis sp., size *Otis tarda* Linnaeus, 1758

Fig. 5A–B

Material. Right ulna, proximal part, AaO-766, and distal part, AaO-767.

Measurements. See Table 7.

Comparison with Recent forms. This fossil was compared with the genera having species of large size today in today Africa: *Ardeotis, Neotis, Lissotis, Afrotis*, and *Otis*. The proximal part of the ulna differs from those of *Ardeotis* because, in that genus, there is almost no separation between the dorsal and ventral cotylae, whereas in the Ahl al Oughlam fossil, as in *Otis*, there is a Crista intercotylaris. On the ventral side, the Impressio brachialis is very deep and forms a fossa which is ventrally bordered by a projecting ridge. In *Ardeotis*, the Impressio brachialis is very wide and extends to the median axis of the bone. In the Ahl al Oughlam fossil, as in *Otis*, the Impressio brachialis is narrower, shallower, not bordered by a ridge, and does not extend to the middle of the cranial face of the shaft.

In the genera *Neotis* and *Lissotis*, the shaft becomes much narrower distally compared to the proximal part, the Impressio brachialis also forms a fossa bordered by a projecting ridge, as in *Ardeotis*. The shaft becomes wider again at the distal part, and the tuberculum carpale strongly projects craniad. In the Ahl al Oughlam fossil, as in the genus *Otis*, the shaft does not become much narrower distally compared to the proximal part.

In the genus *Afrotis*, the shapes of the cotylae are different. The dorsal cotyla is almost as wide as the ventral cotyla and has the shape of a parallelogram, whereas in the Ahl al Oughlam fossil, as in *Otis*, the dorsal cotyla is much narrower than the ventral cotyla.

Compared to a Recent *Otis tarda*, in the fossil the olecranon is less proximally projecting and narrower at its base, and the dorsal cotyla is prolonged distally on the cranial face by a shorter lip. At the distal part, the shape of the articular surface is craniocaudally narrower, and both dorsal and ventral condyles are more distally projecting than in the Recent form. The same characteristic has been described for an *Otis* sp. from the upper Pliocene of Saint-Vallier, the age of which is similar (Mourer-Chauviré, 2004, fig. 4). Finally, the Tuberculum carpale is situated further in the proximal direction and is dorsoventrally narrower than in the Recent form. The Papillae remigales, or quill knobs, are often very projecting in the Otididae. On the caudal face of the proximal part one can see three papillae, the first one slightly flattened, the other ones circular and very projecting.

Comparison with fossil forms. *Otis lambrechti* Kretzoi, 1941, a species comparable in size to *Otis tarda*, has been reported in several southern European localities (Hungary, Romania, Austria) dated from MN 18 to MNQ 22 (Mourer-Chauviré, 2004), but no ulna was found in any of these localities. A larger form, *Iorotis gabunii* Burchak-Abramovich & Vekua, 1981, has been described from the Pliocene (MN 16) of oriental Georgia, but it is larger than the Recent males of *O. tarda*. The other extinct species of the genus *Otis* are smaller than *Otis tarda*.

Genus *Chlamydotis* Lesson, 1839

Chlamydotis sp. cf. *C. mesetaria* Sánchez-Marco, 1990

Fig. 5C–E

Material. Right tarsometatarsus, proximal part and shaft, AaO-2664.

Measurements. See Table 8.

This tarsometatarsus shows the morphological characteristics of the genus *Chlamydotis* as follows. There is a strong difference in level between the lateral and the medial cotylae. The lateral cotyla is offset clearly lower in the distal direction than the medial cotyla. The lateral cotyla has an almost octogonal shape. It has two articular facets on its lateral side, a cranial one and a plantar one. There is a small groove on the cranial side of the medial cotyla, on the medial side of the Eminentia intercotylaris. In the hypotarsus there is a large roofed groove. The Crista medialis hypotarsi does not project plantarly as far as in the genus *Otis*, but it is extended by a straight ridge on the medioplantar side.

At the present time, the genus *Chlamydotis* only includes one species, *Chlamydotis undulata*, the Houbara bustard, but an extinct species, *C. mesetaria*, has been described from the locality of Layna, Spain (Sánchez-Marco, 1990), dated to be from the end of the mammal reference-level MN 15, or about 3.5 Ma (Daams *et al.*, 1999). This species is only known by a tibiotarsus. It is characterized by a slightly larger size than in the Recent species *C. undulata*, and the width of the shaft in the middle, as well as just proximally to the condyles, shows that it was a proportionally more robust form. In the Ahl al Oughlam form, the measurements are very slightly larger than in the Recent species, but the shaft is clearly stronger. For that reason we designate it as *Chlamydotis* sp. cf. *C. mesetaria*, the age of which is also comparable.

Table 8. Measurements (mm) of fossil *Chlamydotis* sp. cf. *C. mesetaria* from Ahl al Oughlam and Recent *Chlamydotis undulata*.

Tarsometatarsus	***Chlamydotis* cf. *mesetaria*** Ahl al Oughlam	***Chlamydotis undulata*** Recent males	Recent females
	AaO-2664	(n=2)	(n=2)
proximal width	15.5	15.8–16.6	13.3–15.3
proximal depth	13.3	13.2–13.2	11.4–12.8
width of shaft at midpoint	ca. 6.3	5.3–5.4	4.8–5.4

A bustard, designated as cf. *Chlamydotis undulata* has been reported from the Middle Miocene of Maboko Island, in Kenya (C. Harrison, 1980).

Genus *Lophotis* Reichenbach, 1839

cf. *Lophotis* sp.

Fig. 5F–G

Material. Almost complete right coracoid, AaO-768.

Measurements (in mm): internal length, 41.4; length from the top of acrocoracoid to the sternal part of the scapular facet, 14.0; proximal width from the medial side of the scapular facet to the lateral side of the glenoid facet, 7.7; least width of shaft, 4.4; depth of shaft at the same level, 3.9; depth of the sternal facet, 4.4.

On this coracoid, the ventral-most tip of the acrocoracoid, the Angulus medialis, and the lateral side of the sternal part are missing. This coracoid has been compared with those of the genera *Tetrax, Eupodotis, Afrotis, Lissotis*, and *Lophotis*, and it is most similar to the genus *Lophotis*. Its morphological chracteristics are as follows: its shape is elongate and more slender than in the other genera; the impression of the M. sternocoracoidei is not strongly indicated; the procoracoid protrudes from the shaft very close to the scapular facet, it is narrow at its base, whereas it is wider in the other genera. In the genus *Lissotis*, the shaft strongly widens in the sternal direction below the scapular facet, whereas this is not the case in the Ahl al Oughlam fossil. Among bustards there is a difference in the shape of the acrocoracoid: in the genera *Tetrax* and *Lissotis* it forms a very long point directed medially and ventrally, whilst in *Afrotis* and *Lophotis* it is shorter, unfortunately it is not possible to see this characteristic on the fossil. This coracoid cannot belong to the same species as the tarsometatarsus referred to *Chlamydotis* sp. cf. *C. mesetaria*: it corresponds to a smaller form. Its dimensions are slightly larger than those of three comparative specimens of *Lophotis ruficrista gindiana* from the USNM.

Order Charadriiformes

Family Charadriidae

Genus *Pluvialis* Brisson, 1760

cf. *Pluvialis* sp.

Material. Left humerus, proximal part, AaO-770.

This humerus resembles *Pluvialis apricaria* and *P. squatarola*. It differs from them because the ledge of the humeral head which overhangs the tricipital fossa is less developed than in these two Recent species. *Pluvialis* aff. *squatarola* has been reported in the Pliocene of the Yorktown Formation (Olson & Rasmussen, 2001). At the present time both species occur on the Atlantic coasts of Morocco.

Genus *Charadrius* Linnaeus, 1758

cf. *Charadrius* sp.

Material. Left humerus, almost complete, AaO-773.

At the present time several species of the genus *Charadrius* occur on the Atlantic coasts of Morocco. According to the estimated length of the humerus (ca. 32 mm) the plover present at Ahl al Oughlam was slightly larger than the Recent species *Charadrius dubius* and *C. alexandrinus* and was closer to the Recent species *Charadrius hiaticula*.

Family Stercorariidae

Genus *Catharacta* Brünnich, 1764

Catharacta sp. cf. *C. skua* Brünnich, 1764

Fig. 5I

Material. Right humerus, distal part and shaft, AaO-4793.

Measurements (in mm): distal width, 18.7; distal depth, 11.5; width of shaft in the middle, 8.5; depth of shaft in the middle, 7.5.

This humerus is morphologically similar to that of the Recent species *Catharacta skua*, and its dimensions agree with that of a Recent specimen from the Paris MNHN as well as with those given by Olson & Rasmussen (2001) for the Recent forms. A *Catharacta* sp., the size of *Catharacta skua* or *C. maccormicki*, has been reported from the Lee Creek Mine, coming probably from the Yorktown Formation (Olson & Rasmussen, 2001). In Florida, the locality of Richardson Road Shell Mine, dating to 2.4–2.0 Ma, has yielded a coracoid of a *Stercorarius* sp., intermediate in size between the Recent species of the genus *Catharacta* and the Recent species of the genus *Stercorarius* (Emslie, 1995). At the present time the Great Skua breeds mainly on islands in the North Atlantic and winters on the continental shelf, on both sides of the Atlantic Ocean and in Western Mediterranean, young individuals reaching Cape Verde Islands and Brazil (del Hoyo *et al*., 1996).

Family Alcidae

Genus *Alca* Linnaeus, 1758

Alca ausonia (Portis, 1889)

Fig. 5J–M

Material. Right humerus, proximal part, AaO-781; left humerus, shaft and distal part, AaO-2666; left scapula, cranial part, AaO-2665; left ulna, distal part, AaO-2667; left radius, shaft and distal part, AaO-841; left carpometacarpus, distal part, AaO-2668; right femur, distal part, AaO-2661; left tibiotarsus, proximal part and shaft, AaO-2693.

This material shows the morphological characteristics of the genus *Alca* and differs from the other members of Alcidae. Alcids are very numerous in the Pliocene of the Yorktown Formation and include, from the smaller to the larger, *Alca* aff. *torda, A. ausonia, Alca grandis* and *Alca stewarti* (Olson, 2007; Wijnker & Olson, 2009). There are no detailed measurements, but it is possible to see that the distal width of the humerus is comprised between ca. 11.8 and 12.8 mm for *Alca ausonia*, and between ca. 13.5 and 14.5 mm for *A. grandis* (Olson & Rasmussen, 2001, fig. 9). In the Ahl al Oughlam specimen the distal part of humerus is incomplete, but it is possible to estimate the distal width (from the cranial face of the Condylus dorsalis to the caudal face of the Epicondylus ventralis) at ca. 11.9 mm. On a cast of the holotype of *Alca ausonia* (IGF 14875), this distal width is 12.3 mm. The Ahl al Oughlam Alcidae is therefore attributed to the extinct species *Alca ausonia*. The measurements are given in Table 9. Compared to a Recent specimen of *Alca torda islandica*, the dimensions of the specimens referred to *Alca ausonia* here from Ahl al Oughlam are on average 24% larger.

In addition to the fossil forms from the Yorktown Formation, alcids belonging to the genus *Alca* have also been reported on the coasts of the Old World. *Alca ausonia* has been described from the Middle Pliocene of Orciano Pisano, in Tuscany, close to the Mediterranean (Delle Cave, 1996). *Alca* sp. has been reported from the Pliocene of El Alamillo, southeast Spain, in marine deposits (Sánchez-Marco, 2003). This form is slightly larger than *Alca torda* and could belong to *Alca ausonia. Alca ausonia* has been reported in the lower Pliocene of the Kattendijk Sands Formation at Kallo, Belgium (Dyke & Walker, 2005). However the total length given for a complete ulna (55 mm) seems too small for this

Table 9. Measurements (mm) of fossil *Alca ausonia* from Ahl al Oughlam.

	Alca ausonia Ahl al Oughlam
Humerus	AaO-781
proximal. width	20.0
depth of humeral head	8.1
Humerus	AaO-2666
maximal distal width	ca. 11.9
max. width of shaft [a]	8.2
max. depth at the same level	4.8
Scapula	AaO-2665
maximal width of omal part	12.7
Ulna	AaO-2667
distal diagonal	ca. 10.5
width of shaft at midpoint	4.4
depth of shaft at midpoint	7.2
Radius	AaO-841
width of shaft at midpoint	4.4
depth of shaft at midpoint	3.0
distal width	6.4
distal depth	4.1
Carpometacarpus	AaO-2668
width major metacarp. at midpoint	3.1
depth major metacarp. at midpoint	4.3
Femur	AaO-2661
width of shaft at midpoint	4.7
depth of shaft at midpoint	4.7
distal width	ca. 9.0
distal depth	ca. 8.6
Tibiotarsus	AaO-2693
proximal width	8.0
proximal depth with crista cnemialis cranialis [b]	12.6
height of crista cnemialis cranialis [c]	8.0
width of shaft at midpoint	4.8
depth of shaft at midpoint	4.0

[a] At 40 mm from the distal end, in proximal direction.
[b] From the facies articularis medialis to the cranialmost part of the crista cnemialis cranialis.
[c] From the articular plane to the tip of the cristal cnemialis cranialis.

species. Four different species of *Alca* (including probably *A. ausonia*) are present in the Early Pliocene (age 3.5 Ma) of the Netherlands (E. Wijnker, pers. comm.).

At the present time alcids still occur on the Moroccan coasts (Urban *et al.*, 1986).

Order Columbiformes

Family Columbidae

Genus *Columba* Linnaeus, 1758

Columba sp. cf. *C. pisana* (Portis, 1889)

Fig. 5H

Material. Right humerus, distal part and shaft, AaO-2672.

Measurements (in mm): distal width, 10.6; distal depth, 7.3; width of shaft in the middle, 5.2.

Given the current environment of Ahl al Oughlam the presence of members of Pteroclidae could be expected, but the humerus AaO-2672 agrees well with the columbids and differs from the pteroclids because in the pteroclids the entepicondyle projects caudad much more than in the columbids, and it is clearly distinct from the ventral condyle.

The species described by Portis (1889) from Orciano Pisano, in Tuscany, as *Falco pisanus*, actually corresponds to a columbid (Mourer-Chauviré, in Olson, 1985c). Mlíkovský (2002) placed this species in the genus *Columba* and he placed it in synonymy with *Columba omnisanctorum* described by Ballmann (1976) from the Gargano. These two species are almost contemporaneous, early Pliocene (MN 14–15) for the Gargano, middle Pliocene (MN 15–16) for Orciano Pisano (Delle Cave 1996). It is not possible to compare these two species directly because they are not represented by the same elements, but they are compatible in size. The ulna of *Columba pisana* is slightly larger than that of Recent *Columba livia* and *Columba oenas*, and the different elements of *Columba omnisanctorum* are included in the range of variation of the Recent *C. oenas* (see measurements in Fick, 1974). *Columba palumbus* is bigger than both species (Fick, 1974). In the Ahl al Oughlam humerus the distal width is 10.6 mm whereas in *C. omnisanctorum* the distal width is 11 mm (Ballmann, 1976).

Columba sp. size *C. palumbus* Linnaeus, 1758

Material. Left carpometacarpus, proximal part, AaO-782.

Measurements (in mm): proximal width, 5.8; proximal depth, 11.2.

The dimensions of this carpometacarpus are larger than those of the Recent *C. livia* and *C. oenas*, and they fall within the range of variation of the Recent *C. palumbus* (see measurements in Fick, 1974).

Order Psittaciformes

Family Psittacidae

Genus *Agapornis* Selby, 1836

Agapornis atlanticus n.sp.

Fig. 5N–Q

Holotype. Almost complete right humerus AaO-786.

Horizon and locality. Late Pliocene, age about 2.5 Ma, Ahl al Oughlam, southeast boundary of the city of Casablanca, Morocco.

Paratypes. Incomplete right humeri, AaO-788, 789, 791, 2670; right humeri, proximal part, AaO-784, 790, 793, 800; right humeri, distal part, AaO-794, 2700, 2701, 2702, 4812; left humeri, AaO-785, 2671; left humeri, almost complete, AaO-783, 787, 853, 854; left humeri, distal part, AaO-2703, 2704, 2705, 2706. The humeri AaO-790, 794, 2700, and 4812 show a deposit of medullary bone.

Referred material. Right ulnae, proximal part and shaft, AaO-797, proximal part, AaO-4814; right ulnae, distal part, AaO-799, 4816; left ulna, almost complete, AaO-792; left ulnae, proximal part, AaO-795, 796, 4815; left ulna, distal part, AaO-4817; right carpometacarpi, almost complete, AaO-775, 776, 778; right carpometacarpus, proximal part, AaO-798; left carpometacarpi, proximal part, AaO-779, 4813.

Diagnosis. Species larger than the Recent or fossil species of the genus *Agapornis*. The humeral head shows a distal extension on the caudal face. On the dorsal side of

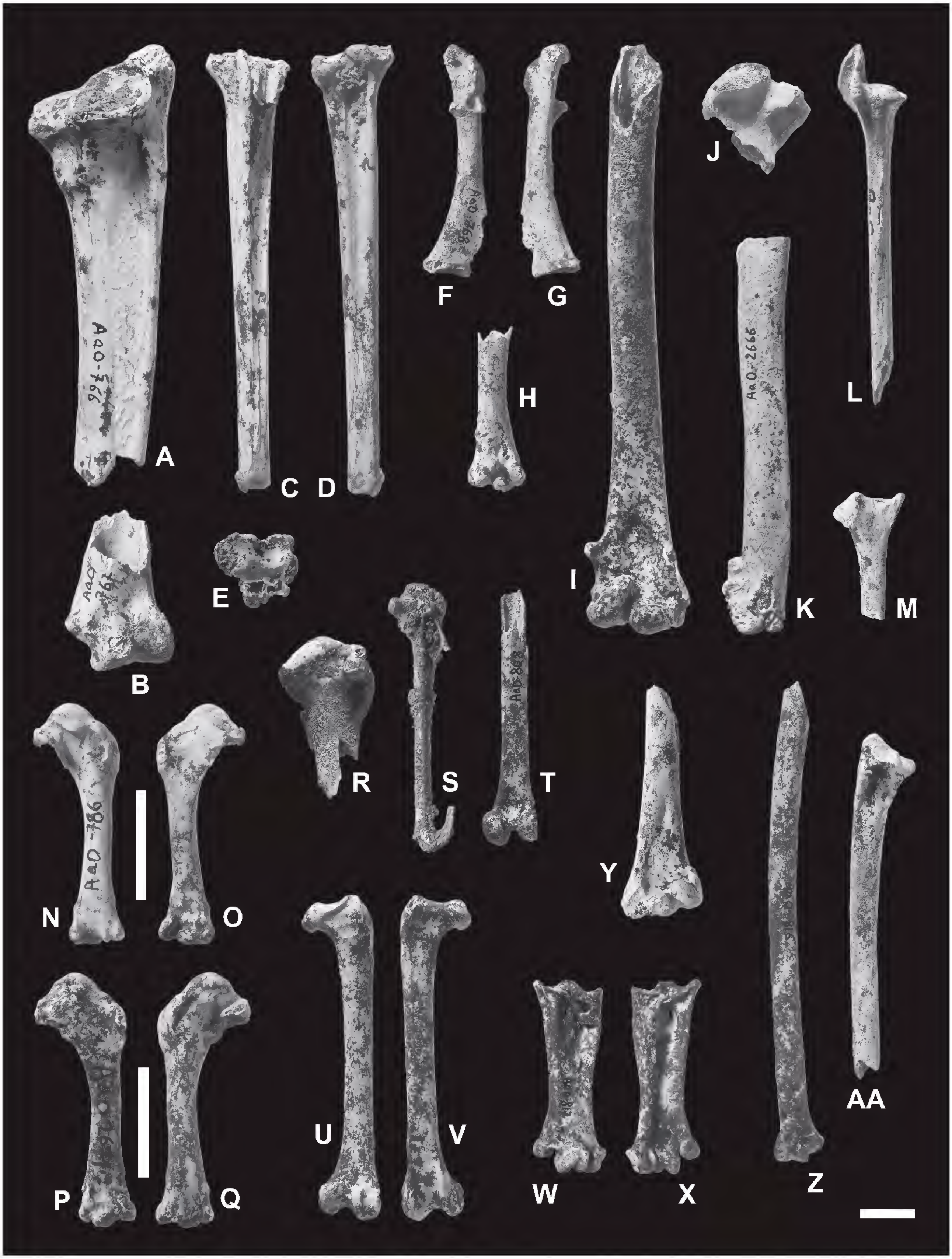

Figure 5. *Otis* sp. size *Otis tarda*, *A–B*: (*A*) right ulna, proximal part, AaO-766, cranial view: (*B*) right ulna, distal part, AaO-767, ventral view. *Chlamydotis* sp. cf. *C. mesetaria, C–E*: (*C*) right tarsometatarsus, proximal part and shaft, AaO-2644, caudal view; (*D*) idem, cranial view; (*E*) idem, proximal view. cf. *Lophotis* sp., *F–G*: (*F*) right coracoid, almost complete, AaO-768, dorsal view; (*G*) idem, ventral view. (*H*) *Columba* sp. cf. *C. pisana*, right humerus, distal part and shaft, AaO-2672, cranial view. (*I*) *Catharacta* sp. cf. *C. skua*, right humerus, distal part and shaft, AaO-4793, cranial view. … [caption continued on facing page]

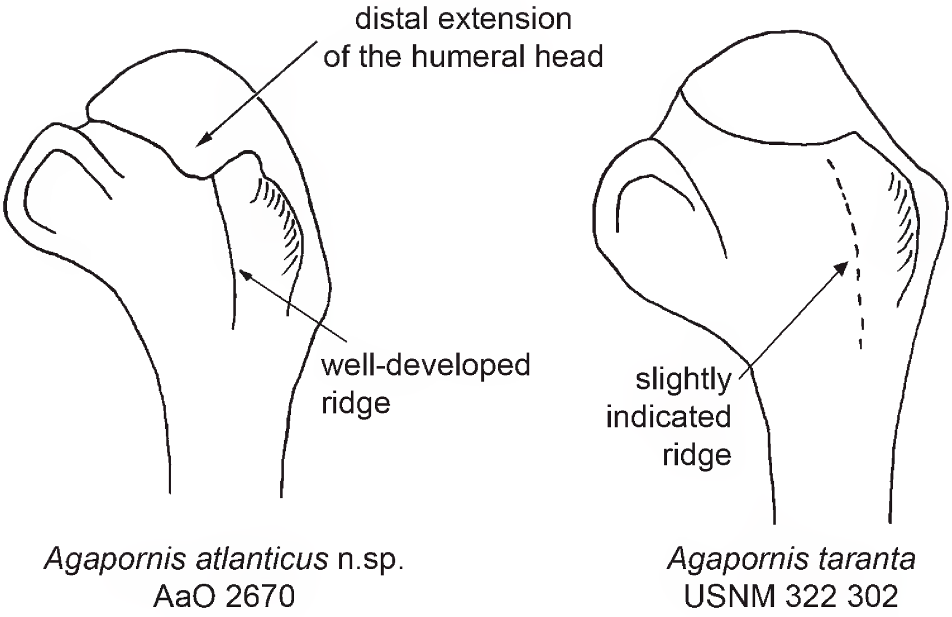

Figure 6. Diagram showing the differences between the proximal humerus of *Agapornis atlanticus* n.sp., from Ahl al Oughlam, and that of a Recent specimen of *Agapornis taranta*, USNM 322302.

the humeral head there is a longitudinal ridge which is more developed than in the Recent species.

Measurements. See Table 10.

Etymology. *atlanticus*, from the Atlantic Ocean, because the locality of Ahl al Oughlam was on the Atlantic shore at the time of the deposit.

Curation of the material. The material will be deposited at the Institut National des Sciences de l'Archéologie et du Patrimoine (INSAP), in Rabat, Morocco.

Description and comparisons. These parrot specimens have been compared with all of the genera that occur in Africa at the present time and which are present in the USNM collection. The fossils can be attributed to the genus *Agapornis*. Among the Recent species of this genus there is a size variation, the smallest one being *A. lilianae*, then by increasing size *A. pullarius, A. personatus, A. fischeri, A. roseicollis*, and *A. taranta*. There was no comparative skeleton of *A. nigrigenis* but this species is similar in size to *A. lilianae*. The Ahl al Oughlam *Agapornis* remains are large and, by their dimensions, they are closer to the Recent species *A. taranta*. Compared to a sample of six individuals of *A. taranta*, the total length of the humerus is similar, but the distal width is smaller and the width of the shaft in the middle is larger in the Moroccan form. In the ulna the mean values of the proximal width and width of shaft in the middle are larger, and for the carpometacarpus the total length and the proximal depth are also larger in the Ahl al Oughlam species.

Morphologically the humerus of *Agapornis atlanticus* differs from the Recent species by the presence of a distal extension of the humeral head on the caudal face. This extension does not exist in the Recent *Agapornis*. There is also a longitudinal ridge that begins on the dorsal side of the humeral head and extends distad. It delimits an elongate fossa, situated between this ridge and the crista m. supracoracoidei. This ridge is very faintly visible in the Recent *Agapornis* (Fig. 6). At the distal end, the attachment of the anterior articular ligament is strongly projecting. Proximal to this attachment, the impression of M. brachialis is situated entirely on the ventral half of the bone. There is a tubercle proximal to the dorsal condyle but it is very slightly indicated and it is visible only on one half of the humeri. This characteristic is different from that described by Stidham for the Recent and fossil *Agapornis* from South Africa, where "the humeri exhibit the character of having a tubercle proximal to the space in between the dorsal and the ventral condyles" (Stidham, 2006, p. 199). In the Ahl al Oughlam parrots the dorsal condyle measures about 2.5 mm proximo-distally and the tubercle is situated about 1 mm proximally to the condyle. This position is different from what we have observed in the genus *Poicephalus* where a tubercle is present and situated proximally to the dorsal condyle, but on the

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Figure 5 [caption continued from facing page]… *Alca ausonia, J–M*: (*J*) right humerus, proximal part, AaO-781, caudal view; (*K*) left humerus, distal part and shaft, AaO-2666, cranial view; (*L*) left tibiotarsus, proximal part and shaft, AaO-2693, lateral view; (*M*) left scapula, cranial part, AaO-2665, lateral view. *Agapornis atlanticus* n.sp., *N–Q*: (*N*) right humerus, almost complete, AaO-786, holotype, caudal view; (*O*) idem, cranial view; (*P*) left humerus, almost complete, AaO-2671, paratype, cranial view; (*Q*) idem, caudal view. *Tyto balearica, R–S*: (*R*) left humerus, proximal part, AaO-4805, caudal view; (*S*) right carpometacarpus, AaO-2684, ventral view. (*T*) *Tyto alba*, left tibiotarsus, distal part, AaO-808, cranial view. *Surnia robusta, U–AA*: (*U*) left femur, AaO-814, caudal view; (*V*) idem, cranial view; (*W*) right tarsometatarsus, almost complete, AaO-817, cranial view; (*X*) idem, caudal view; (*Y*) left humerus, distal part, AaO-839, cranial view; (*Z*) left ulna, distal part and shaft, AaO-816, ventral view; (*AA*) left ulna, proximal part and shaft, AaO-815, ventral view. The scale bars represent 1 cm. Same scale bar for *A–M* and *R–AA*.

Table 10. Measurements (mm) of fossil *Agapornis atlanticus* n.sp. from Ahl al Oughlam and Recent *Agapornis taranta* (s = standard deviation).

	***Agapornis atlanticus* n.sp.** Ahl al Oughlam				***Agapornis taranta*** Recent			
	mean	observed range	n	s	mean	observed range	n	s
Humerus								
total length	22.50	22.0–23.4	8	0.53	22.78	21.7–23.8	6	0.78
prox. width [a]	7.37	7.1–7.6	7	0.20	—	—	—	—
distal width	4.83	4.7–5.0	11	0.12	5.08	4.8–5.4	6	0.26
width of shaft at midpoint	2.68	2.4–2.9	13	0.16	2.05	1.9–2.3	6	0.14
Ulna								
total length	ca. 27.0	—	1	—	27.67	26.5–28.7	6	0.84
prox. width	4.00	3.9–4.1	4	0.08	3.78	3.5–4.0	6	0.19
width of shaft at midpoint	2.00	1.9–2.1	4	0.12	1.93	1.9–2.1	6	0.08
Carpometacarpus								
total length	21.20	21.0–21.4	2	0.28	17.48	16.6–18.7	6	0.78
prox. depth	5.58	5.5–5.7	4	0.10	4.70	4.4–4.9	3	0.26

[a] From the ventral side of the crista bicipitalis to the dorsal side of the crista m. supracoracoidei.

median side of this condyle and closer to it.

Extinct psittacids exist in the Neogene of the Palaearctic region, such as *Archaeopsittacus verreauxi*, from the early Miocene of Saint-Gérand-le-Puy (MN 2a) (Milne-Edwards, 1867–1871), *Xenopsitta fejfari* from the early Miocene of Merkur (MN 3) (Mlíkovský, 1998a), and *Pararallus dispar* (syn. *Psittacus lartetianus*) from the middle Miocene of Sansan (MN 6) (Cheneval, 2000). Indeterminate psittacids have also been reported in the middle Miocene of the Nördlinger Ries (MN 6) and of Steinheim (MN 7) (Heizmann & Hesse, 1995). In Africa, psittacids were present in the late Miocene and the early Pliocene of Langebaanweg (Rich, 1980; Stidham, 2006), and *Agapornis* sp. is reported from two localities of Olduvai, Bed I, lower Pleistocene (Brodkorb, 1985), and from the Pleistocene of Kromdraai B (Stidham, 2006).

The presence of an *Agapornis* species in Morocco is surprising because all of the Recent species of this genus live South of the Sahara, and most of them have a very limited distribution area in the southern part of the African continent. These different species live in variable environments, moist savannah, lowland primary and secondary forests, montane forests, wooded steppe (Fry *et al*., 1988), but one species, *A. roseicollis*, lives close to the western coast of Southern Africa (Angola, Namibia, South Africa) in dry wooded and subdesert steppe. This species may sometimes nest in rock crevices. The presence of medullary bone (Rick, 1975) inside the medullary cavity of several humeri indicates that *Agapornis atlanticus* was nesting in the vicinity of the fossiliferous site. It it possible that this species nested in the blocks of consolidated sands in which the fossils were deposited, while the other species of this genus nest in termitaria or in trees (Fry *et al*., 1988).

Order Strigiformes

Family Tytonidae

Genus *Tyto* Billberg, 1828

Tyto balearica Mourer-Chauviré, Alcover, Moya & Pons, 1980

Fig. 5R–S

Material. Left humerus, proximal part, AaO-4805; left ulnae, proximal parts, AaO-4794, 4806; left radii, distal parts, AaO-852, 2686; right carpometacarpus, almost complete, AaO-2684; left carpometacarpus, distal part, AaO-2685; right tibiotarsus, distal part, AaO-2698; left tibiotarsi, distal parts, AaO-4807, 4808.

Measurements (in mm): humerus, proximal width, ca. 17.0; proximal depth, 9.8. Ulnae, proximal width, 9.9 and 10.1. Radii, least width of shaft, 2.8 and ca. 2.9. Carpometacarpus, total length, est. 48.5. Tibiotarsi, distal width, 10.7 and 11.2.

The dimensions of these elements are clearly larger than those of the Recent *Tyto alba* and they are either included in the size-variation of the extinct species *T. balearica*, or are close to them (Mourer-Chauviré & Sánchez-Marco, 1988; Louchart, 2002). *Tyto balearica* was described from three insular localities of the Balearics (Mourer-Chauviré *et al*., 1980), then was found again in several continental localities of Spain and the south of France, where it is present until the Plio-Pleistocene boundary (summary statement in Sánchez-Marco, 2001). It has also been found in the Middle Pleistocene of Corsica and Sardinia where it is represented by a particular subspecies, *T. balearica cyrneichnusae* (summary statement in Louchart, 2002). On the other hand, the remains from the upper Miocene of Aljezar B (MN 12) (Cheneval & Adrover, 1993), of Valdecebro (MN 12) (Sánchez-Marco, 2001), and some remains from the Mio-Pliocene of Gargano referred by Mlíkovský (1998b) to *T. balearica*, do not belong to this species (Louchart, 2002).

Tyto balearica is thus known during a time span extending from the Early Pliocene (MN 15) to the Middle Pleistocene. In all these localities it does not coexist with *Tyto alba*. The only locality where *T. balearica* is found together with another species of the genus *Tyto* is the Middle Pleistocene locality of Castiglione 3 CG, in Corsica, where an indeterminate species of *Tyto* is represented by a pedal phalange (Louchart, 2002).

Tyto alba (Scopoli, 1769)

Fig. 5T

Material. Left ulna, distal part and shaft, AaO-801; distal part, AaO-850; right radii, distal parts, AaO-802, 803; right carpometacarpus, distal part, AaO-805; left carpometacarpi, proximal part, AaO-806, distal part, AaO-4797; right femora, shaft, AaO-804, distal part, AaO-807; right tibiotarsi, distal part and shaft, AaO-4799; left tibiotarsi, distal parts, AaO-808, 809, 810; right tarsometatarsi, proximal part, AaO-813, distal parts, AaO-849 (juvenile), 4803; left tarsometatarsi, proximal part, AaO-2699, distal part, AaO-812, shaft AaO-811.

The dimensions of the Ahl al Oughlam Barn Owl are slightly larger than the maximal values for a population of Recent *Tyto alba alba* and *T. alba guttata* (Louchart, 2002) but there are a large number of subspecies with strong size variation. The Recent species *Tyto alba* has been reported in the Middle Miocene (MN 7, Mein 1990) of Beni Mellal in Morocco (Brunet, 1971) but it is only represented by an alar phalange (Brunet, 1961). It cannot be excluded that this phalange could have belonged to an earlier species of the genus *Tyto*, as for example *Tyto sanctialbani*, the dimensions of which are similar to those of the Recent *Tyto alba* (Lydekker, 1893). Apart from this reference, the oldest mention of the presence of *Tyto alba* is from the locality of Olduvai, Bed I, dating between 1.85 and 1.70 Ma (Brodkorb & Mourer-Chauviré, 1984a).

Family Strigidae

Genus *Surnia* Duméril, 1806

Surnia robusta Janossy, 1977

Fig. 5U–AA

Material. Rostrum maxillare, AaO-818; left humerus, distal part, AaO-839; left ulnae, proximal part and shaft, AaO-815, distal part and shaft, AaO-816; left femur, AaO-814; right tarsometatarsus, almost complete, AaO-817 (only the Crista medialis hypotarsi is missing).

Measurements. See Table 11.

Table 11. Measurements (mm) of *Surnia robusta* from Ahl al Oughlam and the Carpathian Basin (Janossy, 1977) and Recent *Surnia ulula*.

	Surnia robusta Ahl al Oughlam	***Surnia robusta*** Janossy, 1977	***Surnia ulula*** Recent, mean
Rostrum maxillare			(n = 6)
length [a]	ca. 15.5	—	9.85
Humerus			(n = 7)
distal width	ca. 15.5	15.5–16.0 [f]	12.16
distal depth	7.8	—	6.10
width of shaft at midpoint [b]	6.3	6.7	4.83
depth of shaft at midpoint [b]	5.5	—	4.40
Ulna			(n = 12)
proximal width	10.2	—	8.02
proximal depth [c]	8.7	—	6.75
distal width [d]	8.6	—	6.75
depth of internal condyle	8.5	—	6.32
width of shaft at midpoint	4.9–5.0	—	3.64
depth of shaft at midpoint	5.1–5.3	—	3.70
Femur			(n = 15)
total length	59.2	—	49.17
proximal width	12.7	—	9.72
proximal depth	8.4	—	6.13
distal width	12.1	12.0	9.39
distal depth	10.1	—	7.71
width of shaft at midpoint	5.2	5.3	4.01
depth of shaft at midpoint	5.5	—	4.05
Tarsometatarsus			(n = 12)
total length	35.3	37.2	25.91
proximal width	12.7	12.6	9.68
partial proximal depth [e]	6.9	—	5.86
distal width	13.3	12.6–15.0 [g]	10.08
distal depth	9.6	—	7.23
width of shaft at midpoint	8.4	7.3	6.05
depth of shaft at midpoint	3.6	—	2.78

[a] Length of the rostrum maxillare from the tip of the rostrum to the cranial border of the nasal aperture.

[b] On the Ahl al Oughlam humerus, the width and depth of shaft are not measured at midpoint, but just distal to the break.

[c] From the cranial border of the ventral cotyla to the top of the olecranon.

[d] From the dorsal border of the dorsal condyle to the top of the tuberculum carpale.

[e] On the Ahl al Oughlam tarsometatarsus the crista medialis hypotarsi is broken. The proximal depth is measured from the dorsal side of the cotylae to the top of the crista lateralis hypotarsi.

[f] n = 3

[g] n = 4

This species was described by D. Janossy from material from four Plio-Pleistocene localities of Hungary (Janossy, 1977; 1983), and it has not been reported from any other locality. It is characterized by its size which is much larger than in the Recent and fossil forms of the species *Surnia ulula*, the Hawk Owl, the only present-day species of the genus *Surnia*.

This material shows the morphological characteristics of the genus *Surnia*, with its particularly short and robust tarsometatarsi. On the rostrum maxillare the ventral face of the os premaxillare is flattened. In the Recent *Surnia ulula* this surface is variable, it is flattened in half of the individuals, and grooved in the other half. The distal humerus shows the same characteristics as are found in the genus *Surnia*. It is strongly ventrally elongated. The impression of M. brachialis is very long and extends very far proximad along the shaft. The ectepicondylar prominence is broken on the fossil, but it is possible to see that it was situated just proximally to the dorsal condyle. In the genus *Surnia*, it is small, but clearly projecting and its top forms a right angle. On the proximal ulna, on the cranial side, distally to the cotylae, the bicipital attachment forms a proximodistally elongated and sharply defined ridge. In the Recent *Surnia ulula*, this ridge projects less and has a variable shape, but it is rather dorsoventrally oriented. The distal ulna does not differ from the Recent *S. ulula* except by its size. The femur also shows the morphological characteristics of the genus *Surnia*. On the femoral head the Fovea lig. capitis is very deep. On the caudal face the lateral condyle extends proximally by a ridge. This ridge closes the Fossa poplitea on its medial side and delimits laterally a deep fossa that is situated proximally compared to the lateral and fibular condyles. On the tarsometatarsus, the Crista medialis hypotarsi is missing. This tarsometatarsus shows the same proportions as in the Recent species, *S. ulula*, but it is larger. Its dimensions are very close to those of the holotype tarsometatarsus of *Surnia robusta*, from Villány 3, which is almost of the same age as Ahl al Oughlam (MN 17, ca. 2–2.5 Ma) (Tyrberg, 1998). The Ahl al Oughlam material has been compared with a sample of 6 to 15 individuals of Recent *S. ulula*, including males and females, from the collections of the MNHN (Laboratoire d'Anatomie comparée and Institut de Paléontologie humaine), in Paris, the NMNH, in Washington, the UCB, in Lyon, and the Paleontological Institute of the Russian Academy of Sciences, in Moscow. On average the postcranial elements of the Moroccan *Surnia robusta* are 31% larger than those of the Recent *Surnia ulula*.

As Janossy has pointed out, the Recent species lives in the taiga zone of Eurasia and North America, and in the mountain regions of Central Asia. "It is a question whether the Lower Pleistocene form had the same ecological significance, in view of the fact that most of the remains originate—as we have seen—from the Submediterranean region of the Villány Mountains" (Janossy, 1977, p. 14). The occurrence of this species at Ahl al Oughlam is not accidental because it is represented by at least two individuals.

Order Passeriformes

A few elements can be attributed to species of the family Alaudidae. Some other elements cannot be identified more accurately, mainly because of the lack of comparative material.

Discussion

It is difficult to compare the Ahl al Oughlam avifauna with the other avifaunas from the upper Miocene and Pliocene of Africa, because these other African faunas include a large proportion of aquatic species, non-marine but living on the shores of rivers and freshwater, saline, or alkaline lakes. In Ethiopia and Chad the late Miocene avifaunas include species belonging to the families Podicipedidae, Phalacrocoracidae, Anhingidae, Ardeidae, Ciconiidae (with large sized forms), Anatidae (with a small sized swan, *Afrocygnus chauvireae*), Gruidae and Heliornithidae (Louchart *et al*., 2005a; Louchart *et al*., 2005b; Louchart *et al*., 2008). Although the Recent African species *Leptoptilos crumeniferus* is not strictly aquatic, forms belonging to the genus *Leptoptilos* are almost always associated with these avifaunas.

The same predominance is found again in the Late Miocene avifaunas of Eastern and Northern Africa. In Kenya the avifauna of Lothagam (Harris & Leakey, 2003) is mainly composed of species of Pelecanidae, Anhingidae, Ciconiidae (*Leptoptilos* cf. *crumeniferus*), Ardeidae, Anatidae and Rallidae. In North Africa, in the Beglia Formation of Tunisia (Rich, 1972), there are species of the families Phalacrocoracidae, Anhingidae, Balaenicipitidae(*Paludiavis richae*, C. Harrison & Walker, 1982), and Ciconiidae (*Leptoptilos richae* C. Harrison, 1974, the size of *Leptoptilos crumeniferus*) (Louchart *et al*., 2005c). In the locality of Sahabi, in Libya, which is probably older than the Mio-Pliocene boundary, there are species of the families Phalacrocoracidae, Anhingidae, Ciconiidae (*Leptoptilos* sp.), and Anatidae [in particular the small swan *Afrocygnus chauvireae* (Ballmann, 1987; Louchart *et al*., 2005a)]. The only locality that has yielded a terrestrial avifauna is Lemudong'o, in Kenya, but the material is very fragmentary and has been only identified at the ordinal or familial level (Stidham, 2007).

The African Pliocene and early Pleistocene avifaunas also include a very large proportion of aquatic forms. In Chad, the avifaunas of Kossom Bougoudi (age 5 Ma) and Koro Toro (age 3–3.5 Ma) only include aquatic forms: phalacrocoracids, anhingids, ardeids, the very large ciconiid, *Leptoptilos falconeri*, and anatids (Louchart *et al*., 2004; Louchart *et al*., 2005c). In Ethiopia, the Pliocene localities of Hadar and Omo have yielded anhingids (Brodkorb & Mourer-Chauviré, 1982) and again the very large ciconiid *Leptoptilos falconeri* (Louchart *et al*., 2005c). In Tanzania, the locality of Olduvai, Bed I, has yielded a great quantity of birds that correspond primarily to aquatic forms, or species of the following families: Podicipedidae, Anhingidae, Phalacrocoracidae, Pelecanidae, Phoenicopteridae, Ardeidae, Balaenicipitidae, Ciconiidae (including possibly *Leptoptilos falconeri*), Anatidae, Rallidae, and charadriiforms belonging to at least seven families (Jacanidae, Rostratulidae, Charadriidae, Scolopacidae, Recurvirostridae, Glareolidae, Laridae) (Brodkorb & Mourer-Chauviré, 1982; Brodkorb & Mourer-Chauviré, 1984b; Brodkorb, 1985). Again in Tanzania, the Upper Pliocene phosphorites of Minjingu have yielded phalacrocoracids (Schlüter, 1991).

In contrast to all these avifaunas with predominant aquatic forms the Pliocene locality of Laetoli, in Tanzania, has yielded bird remains and fossil eggs belonging only to terrestrial forms (Struthionidae, Accipitridae, Phasianidae, Numididae, Columbidae and Strigidae) (Watson, 1987; T. Harrison, 2005; T. Harrison & Msuya, 2005). In South Africa, in the locality of Langebaanweg, the Quartzose Sand Member, lower Pliocene, has yielded a very rich avifauna where the most abundant birds are species of Phasianidae (58% of the Minimal Number of Individuals = MNI). Among the aquatic forms, procellariiforms and charadriiforms are relatively numerous (8% of the MNI), but other families were represented by only 1% (Phalacrocoracidae) or less than 1% (Spheniscidae, Podicipedidae, Sulidae, Ciconiidae, Rallidae) of the MNI (Rich 1980), and the ardeids, phoenicopterids and balaenicipitids are not represented (Olson, 1985b). Another difference is the presence of a large, extinct, stork, *Ciconia kahli* (Haarhoff, 1988), whereas in the other upper Miocene and Pliocene localities of Africa, the ciconiids are represented by very large forms of Leptoptilini (genera *Leptoptilos* and *Ephippiorhynchus*) (Louchart *et al*., 2005c; Louchart *et al*., 2008).

The Ahl al Oughlam avifauna is made up partly of marine forms and partly of terrestrial forms. The marine forms are: *Phoebastria anglica, Phoebastria* sp. cf. *P. albatrus, Phoebastria* sp. cf. *P. nigripes, Calonectris* sp. cf. *C. diomedea, Pelagornis mauretanicus, Morus peninsularis, Morus* sp. cf. *M. bassanus, Catharacta* sp. cf. *C. skua*, and *Alca ausonia*. Among the terrestrial forms, it is possible to distinguish forms whose recent or past distribution can be both Eurasiatic and African, or Palaearctic, or only African. The Eurasiatic and African forms are: *Struthio asiaticus, Geronticus olsoni* n.sp., *Alopochen* sp. cf. *A. aegyptiacus, Tadorna tadorna, Otis* sp. size *O. tarda, Chlamydotis* sp. cf. *C. mesetaria, Columba* sp. size *C. palumbus, Tyto alba*. The Palaearctic forms are: *Mergus* sp., the genus *Plioperdix, Columba* sp. cf. *C. pisana, Tyto balearica*, and *Surnia robusta*. The uniquely African forms are: cf. *Lophotis* sp. and *Agapornis atlanticus* n.sp.

The marine avifauna of Ahl al Oughlam is very similar to the slightly older avifauna of the Yorktown Formation, North Carolina, and it is very different from the Early Pliocene avifaunas of South Africa (Langebaanweg, Olson, 1985d, and Duinefontein, Olson 1985a). A very rich marine avifauna from the Early Pliocene of Netherlands (about 3.5 Ma) is currently under study by Erik Wijnker. It also presents great affinities with the Yorktown Formation avifauna (E. Wijnker, pers. comm.). The marine avifauna of Ahl al Oughlam, with its three species of albatrosses, one extinct, and the other two closely related to Recent forms of the North Pacific, and the most recent member of Pelagornithidae known so far, is very different from the present day avifauna and shows that there has been a considerable modification in the Atlantic avifauna since the end of the Pliocene. However, this modification occurred progressively because albatross colonies were still present in the North Atlantic until the Middle Pleistocene (Olson & Hearty, 2003).

Among the mammals, most of the genera identified at Ahl al Oughlam are also known in Eastern or Southern Africa (Geraads, 2006). Unlike the mammals, the terrestrial bird fauna does not look like the other terrestrial avifaunas from the Pliocene of Africa, with the exception of the ostriches, which are present in almost all the localities. In particular, galliforms are represented at Ahl al Oughlam by the Eurasiatic genus, *Plioperdix*, whereas the African Pliocene avifaunas generally include species of the genus *Francolinus*, and sometimes *Coturnix* (Brodkorb, 1985), or *Pavo* (Louchart, 2003; Pickford *et al.*, 2004). This shows that, as far as the birds are concerned, Morocco already belonged to the palaearctic zoogeographical region in the late Pliocene. The only really African elements are a bustard, referred to the genus *Lophotis*, and the small *Agapornis* parrot. The avifauna does not include any oriental component.

Paleoecological significance

The pollen record of the ODP site 658, situated at 21°N, makes it possible to follow the evolution of the vegetation over a long period, from 3.7 Ma to 1.7 Ma (Leroy & Dupont, 1994). According to these authors (1994, p. 309) "The oxygen isotope record of ODP Site 658 shows high glacial values for stages 104 (2.60 Ma), 100 (2.53 Ma) and 98 (2.49 Ma) resembling the strong fluctuations of the Quaternary. These stages are expressed in the pollen spectra by high percentages of dry elements, such as Amaranthaceae-Chenopodiaceae, Caryophyllaceae, *Artemisia* and *Ephedra*. During this period, probably desert vegetation developed in Northwestern Africa, as a response to severe aridification in combination with increased trade winds". The ODP site 658 is situated too far away from the Casablanca region to give information about the vegetation of this region, but nevertheless it indicates a growing aridification of northwestern Africa during this period. This is confirmed also by what is known in the Mediterranean area where a first steppe appears at about 2.5 Ma, indicating a cooler and more arid climate.

As already mentioned the marine avifauna of Ahl al Oughlam is very similar to the slightly older avifauna of the Yorktown Formation, which is situated almost at the same latitude (35°23'22"N, Olson & Rasmussen, 2001), and it does not indicate anything concerning the temperature. The mammals, by the absence of tree-dwelling monkeys, the virtual absence of forest or even woodland antelopes, and the abundance of gerbillids, point to an open landscape (Geraads, 2006). Most of the landbirds, with the presence of ostriches, ibises, bustards, small partridges, larks, also correspond to an open environment. The abundance of the small parrot, *Agapornis atlanticus* n.sp., is surprising, but in the genus *Agapornis* one species, *A. roseicollis*, lives in dry wooded and subdesert steppes (Fry *et al.*, 1988). The oddest element is the presence of the genus *Surnia*, the only Recent species of which, *Surnia ulula*, lives in the forest tundra and boreal taiga of the North of the Holarctic region and the mountains of Central Asia, but avoids the dense coniferous forests (del Hoyo *et al.*, 1999). At the present time forests of cork-oaks and holm oaks are present in the El Katouat massif, to the South East of Casablanca, which reaches its highest point at 1058 m, but this massif is situated at about 60 km from the site. It seems therefore probable that the ecological requirements of the extinct species *Surnia robusta* were different from those of the Recent species *Surnia ulula*.

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Late Pliocene Avifauna from the Hominid Bearing *Zinjanthropus* Land Surface at Olduvai Gorge, Tanzania

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ABSTRACT. Taxonomic and taphonomic data on 236 fossil bird bone specimens are applied to paleolandscape models and reconstructions developed by the Olduvai Landscape Paleoanthropology Project (OLAPP) for Late Pliocene (1.84 Ma) hominid bearing deposits in the FLK Complex at Olduvai Gorge, Tanzania. Shorebirds dominate the avifauna but the occurrence and densities of different avian ecotypes vary across the landscape in ways that corroborate OLAPP reconstructions of wetland, peninsular and riverine landscape facets in this area of the paleo-Lake Olduvai Basin. Taphonomic profiles are based on observations of modern bird bone in similar environments of Tanzania. The taphonomy suggests habitat patchiness within these delineated landscape facets. Results support the use of fossil bird assemblages, even small assemblages thereof, for aiding in and refining paleoenvironmental reconstructions.

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Olduvai Gorge is a bifurcated valley in the Eastern Serengeti Plains, part of the western margin of the Eastern Rift Valley of northern Tanzania. The Ngorongoro Volcanic Highlands to the south and east contributed ca. 100 m of volcaniclastic sediments spanning the last two million years at Olduvai (Hay, 1976). This produced extensive, fossiliferous deposits, dating from the late Pliocene through more recent times, which were later exposed by tectonic uplift and down-cutting that created the Gorge.

Olduvai Gorge is best known for its paleoanthropological richness, beginning with discoveries by Louis and Mary Leakey (e.g., L.S.B. Leakey, 1965; M.D. Leakey, 1971) of early hominid fossils in association with primitive, Oldowan stone tools. Since 1989, excavations at Olduvai have been undertaken by the Olduvai Landscape Paleoanthropology Project (OLAPP), an international and interdisciplinary team whose goals are to understand the subsistence ecology of these early hominids through detailed reconstructions of the paleoenvironments in which they made and used stone tools and butchered animal carcasses (e.g., Blumenschine & Masao, 1991; Peters & Blumenschine, 1995; Blumenschine & Peters, 1998; Blumenschine *et al*., 2008). OLAPP uses a landscape paleoanthropology approach in which numerous, relatively small scale excavations are placed across exposed portions (ca. 130 km^2) of the Olduvai Basin. Trench locations are based on accessibility of the target stratigraphic unit-regardless of artifact densities observed to have been eroded to the surface. This method produces samples of stone tools, fossils and other paleoenvironmental indicators across a full range of paleolandscape facets for a given depositional sequence.

A recent focus of OLAPP has been to develop landscape samples between and beyond two important Late Pliocene (1.84 Ma) sites in the FLK Complex (Fig. 1): Level 22 at

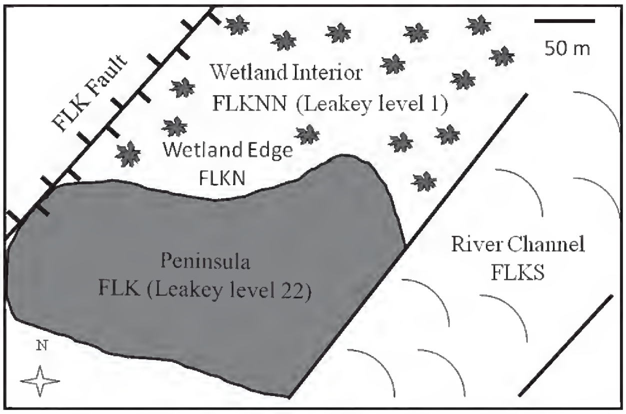

Figure 1. Schematic map depicting the spatial orientation of three major landscape facets in the FLK Complex, during Middle Bed I times (1.8 Ma). Landscape reconstructions are based on botanical, sedimentological and paleontological material recovered by OLAPP in the areas of FLK S (Tr. 143, 146, 148), FLK (Tr. 138, 140, 141), FLK N (Tr. 137, 144, 142, 147), and FLK NN (Tr. 134, 135, 145) (Blumenschine *et al*., in press) and by the M.D. Leakey's (1971) at FLK (Level 22) and FLK NN (Level 1). Birds were recovered from all trenches with the exception of 134, 141, 143 and 148.

FLK and Level 1 at FLK NN. These sites were excavated by the Leakeys in 1959–1962 and are known for their dense concentrations of Oldowan stone artifacts and vertebrate fossils, including hominid remains such as the type specimens of *Homo habilis* and *Paranthropus* (syn. *Zinjanthropus) boisei*, (L.S.B. Leakey, 1959; L.S.B. Leakey *et al*., 1964; Tobias, 1967). The FLK Complex spans a distance of ca. 0.5 km along the eastern lake margin, or floodplain, of paleo-Lake Olduvai, a closed, shallow, saline and alkaline lake that fluctuated in size between a maximum diameter of ca. 25 km during wet periods, and a perennial portion of ca. 10 km diameter during dry periods (Hay, 1976). The deposits of interest occur on what is referred to as the *Zinjanthropus* land surface, named for the famous *Zinjanthropus* skull discovered in 1959 from FLK, Level 22 (L.S.B. Leakey, 1959). This land surface is stratified between two volcanic tuffs, IB and IC, the latter of which buried and preserved the *Zinjanthropus* land surface, allowing for geologically precise dating of the *Zinjanthropus* land surface to landscape formation between 1.845 + 0.002 Ma and 1.839 + 0.005 Ma (based on dates in Blumenschine *et al*., 2003).

OLAPP has identified several paleolandscape facets along this half-kilometer stretch of the *Zinjanthropus* land surface (Fig. 1) on the basis of sedimentary facies analysis and supported by botanical and vertebrate fossils (Blumenschine *et al*., in press). These landscape facets include a 0.5–1.0 m high, lightly wooded Peninsula in the area of FLK, with a very low-gradient River Channel or Spillway to the south (FLK S) and a freshwater Wetland (FLK N and FLK NN), directed towards the lake shoreline to the north. The Wetland is divided into two sub-facets, an expansive Wetland Interior (FLK NN), located along the eastern lake margin, and the Wetland Edge (FLK N), a narrow zone occurring at the ecotone of the Wetland and Peninsula. These four landscape facets delimit for the first time the mosaic of marshland, woodland, bushland and grass/sedgeland environments evident from previous analyses of mammalian faunas from the two Leakey sites (e.g., Plummer & Bishop, 1994; Kappelman *et al*., 1997; Fernandez-Jalvo *et al*., 1998), as well as OLAPP's results (Blumenschine *et al*., in press).

The fossil avifauna from the *Zinjanthropus* land surface contributes two classes of paleoecological information to these landscape reconstructions. One is the taxonomic and ecotypic composition of avifaunal assemblages from each landscape facet. A second is comprised of taphonomic data from the same assemblages, the interpretation of which are guided by my observations in modern saline-alkaline lake environments in the Rift Valley of northern Tanzania (Prassack, dissertation in prep.). Here, I report these taxonomic and taphonomic data, providing details not reported in Blumenschine *et al*. (in press).

Materials and methods

Fossil bird bones (NISP [number of identified specimens present] = 236) were recovered from the *Zinjanthropus* land surface in nine of the thirteen trenches excavated by OLAPP during the 2006–2008 field seasons. Excavations were made by skilled OLAPP field workers using picks to break up the matrix followed by dry sieving using a 5 mm wire mesh sieve. For trenches 144–147, blocks of clay were taken back to the base camp where they were spread on plastic sheets, wetted, and allowed to dry in several cycles to break up the matrix, allowing the recovery of micro-faunal remains with low risk of breakage and higher likelihood of recovery. Taxonomic identifications are conservative and based on comparison to multiple osteological specimens from a full range of relevant modern taxa housed at the Florida Museum of Natural History and American Museum of Natural History. Specimens were not piece-plotted during excavation, such that in–situ specimen associations could not be made. As a result, I made no attempt to identify phalanges or vertebrae beyond that of Aves. Shorebird identifications are to the family level only until a more comprehensive comparative analysis can be made of these specimens.

Ericson's (1987) formula for measuring wing versus leg abundance is used to determine if taphonomic processes affected avian skeletal part survivorship and how this may have differed across the landscape. In this formula, the NISP of wing elements (humerus + ulna + carpometacarpus) is divided by the sum of wing and leg (femur + tibiotarsus + tarsometatarsus) elements, such that a percentage deviation of the quotient from 50% suggests taphonomic bias in skeletal part survivorship.

Taphonomic analysis involved careful examination of each specimen under a 100 W lamp using 10–20× magnification hand lenses. Flaking, cracking and corrosion of bone (Fig. 2) was used to assign bone to subaerial weathering stages (Table 2) following Behrensmeyer (1978) with proper adjustment for birds (Behrensmeyer *et al*., 2003). Evidence of carnivore tooth marks (Fig. 3a–b, Blumenschine *et al.,* 1996), rodent gnawing (Fig. 3c), medullary bone (Fig. 3d), and trample marks (Behrensmeyer *et al*., 1986; Fiorillo, 1989) was also noted. Bioerosion, defined here as the macroscopic alteration of bone's outer cortical surface by algae, fungi, aquatic invertebrates and/or insects (see Blumenschine *et al*., 2007 for review), was diverse and observed on specimens from all facets. Data on bioerosion will be presented in a forthcoming manuscript, comparing fossil marks to those observed during modern landscape studies in Tanzania (Prassack, dissertation in prep.).

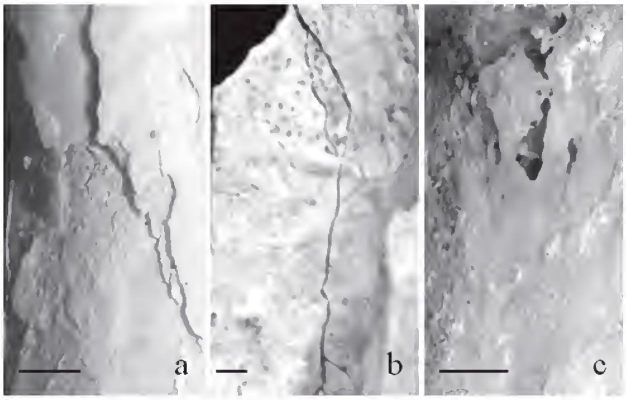

Figure 2. Flaking (*a*), cracking (*b*), and corrosion (*c*) to bird bone interpreted as the result of exposure to subaerial weathering. Scale bars are 5 mm (*a*), 1 mm (*b*), and 5 mm (*c*).

Results

Table 1 lists the 236 fossil bird specimens recovered by OLAPP in the FLK Complex. The vast majority of specimens (70%) are too fragmented or lacking in sufficient diagnostic criteria for identification beyond Aves. Of the 70 specimens that could be identified further, shorebirds (Charadriiformes) are the most common ecotype (57%), and are found in all landscape facets. However, a variety of lake and wetland taxa, including grebes, rails and ducks and birds typical of bush, grass, and open wood land, are also represented. Shorebird medullary bone is present in the Wetland Interior and Wetland Edge.

Taphonomic results for each of the four landscape facets are presented in Table 2. Appendicular elements are more common than axial elements (56.8% of total assemblage), and wing bones are more common than those from the leg (65.7%). Weathering is low across all facets, with 72% of the FLK Complex avifauna being described to stage 0–1. The incidence of more heavily weathered specimens increases across the landscape from the Wetland Interior to the Channel, with 23.7% of Wetland Interior bones being at stage 2 or higher compared to a value of 46.2% in the Channel facet. Within the Wetland Interior, weathering is higher at Trench 145 than at Trench 135, and preservation was so poor that no bones could be identified beyond Aves. On the Peninsula, bones are slightly more weathered and corroded at Trench 140 than at Trench 138. Leg bones are both more likely to be weathered beyond stage 1 (34.8%) than wings (12.5%). Carnivore tooth-marked bones are found in all facets (27% total assemblage), but are most common on the Peninsula (39.3%). Legs are more commonly tooth-marked (38%) than wings (26.4%). Rodent gnawing (7.6%) and trampling (4.9%) are uncommon and primarily limited to the Peninsula and Channel. Bioerosion occurs in all facets but the type of modification varies across facets. Types of bioerosion observed include yellow oblong marks, clusters of tiny black dots, stained cracks, and both isolated and branching smooth-bottomed runnels that penetrate through the upper layer of the outer cortical surface. Dendritic-patterned stains produced by manganese dioxide are evident on specimens from all facets, but are most common on the Peninsula.

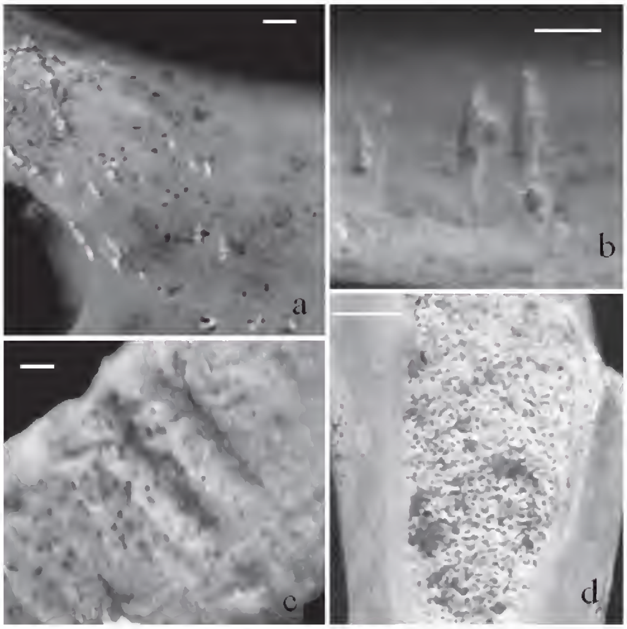

Figure 3. Taphonomic analysis of the FLK Complex birds revealed modifications by carnivores including (*a*) small tooth pits and (*b*) scores, in all landscape facets. Rodent-gnawed bones (*c*) also occurred in all facets, while medullary bone (*d*) was limited to the Wetland Interior and Wetland Edge. Scale bars are 1 mm.

Discussion

The dominance of shorebirds among the *Zinjanthropus* land surface avifauna, and their occurrence in all landscape facets, may reflect the complex's proximity to the shoreline of paleo-Lake Olduvai, but shorebirds can be found in a wide range of habitats (i.e., shoreline, wetland edge, flooded grassland, and open savanna). Future refinement of the shorebird taxonomy for this complex is expected to better reflect known habitat preferences of each species. For example, shorebird density is highest in the Wetland Interior, comprised of small sandpipers and plovers, such as are typically found in modern near-shore marshes. Shorebird numbers decrease away from the Marsh Interior and are replaced by larger taxa, likely those associated with wetland and riverine systems (e.g., *Glareola, Limosa, Pluvialis*). Ducks, rails and grebes are also well represented in the complex but are primarily limited to the Wetland Edge and Peninsula, as would be expected given the habitat preferences of these taxa. Larger birds (e.g., flamingo, stork, cormorant, goose and pelican) were only found in OLAPP samples from the Channel facet (i.e., a large extinct goose-like duck and midshaft fragments of a large bird) although Matthiesen (1990) reports them at FLK Level 22 (Peninsula) and FLK NN Level 1 (Wetland Interior). I have also recovered larger birds from other Bed I strata.

Low overall weathering supports Behrensmeyer *et al.*'s (2003) suggestion that bird bone peaks at weathering stage 1, while mammal bone weathering typically peaks at stage 2. Differences across the landscape may reflect differences in vegetative ground cover and/or soil chemistry. Tooth-marked bird bones comprise 27% of the entire FLK Complex avian assemblage, a percentage similar to both modern, carnivore-ravaged bird bone assemblages and

Table 1. NISP (number of identified specimens present) for avifauna recovered from the four landscape facets reconstructed by OLAPP in the FLK Complex, Olduvai Gorge, Tanzania. Charadriiformes are only assigned to family level and general body size (i.e., *Calidris alba* and *Charadrius tricollaris* would be considered small sandpipers and plovers respectively). Numbers in parentheses denote NISP for taxa identified beyond that of Aves.

area in FLK Complex		FLK S Tr. 146	FLK Tr. 138, 140	FLK N Tr. 137, 142, 144, 147	FLK NN Tr. 135, 145	total NISP
landscape facet		Channel	Peninsula	Wetland Edge	Wetland Interior	
Charadriiformes indet.		—	2	6	2	10
Scolopacidae						
	small sandpipers	1	—	9	10	20
	large sandpipers	—	1	1	—	2
Charadriidae						
	small plovers	1	—	1	3	5
	large plovers	—	—	1	—	1
Recurvirostridae		—	—	2	—	2
Podicepidae						
	Tachybaptus ruficollis	—	—	5	—	5
	Anatidae					
	Anatidae indet.	1	1	1	—	3
	Anas crecca	—	1	2	—	3
	Aythyia sp.	—	1	—	—	1
Rallidae						
	Rallidae indet.	1	—	—	—	1
	Amaurornis flavirostris	—	—	1	—	1
	Sarothrura cf. sp.	—	—	1	—	1
	Porphyrio alleni	—	1	—	—	1
	Gallinula chloropus	—	—	1	—	1
Ardeidae						
	Ardeidae indet. (small)	—	—	1	—	1
Corvidae						
	Corvidae indet.	—	1	—	—	1
Columbidae						
	Streptopelia decipiens	1	1	3	1	6
Colidae						
	Colius cf. sp.	—	—	1	—	1
Pstittacidae						
	Agapornis cf. sp.	—	—	1	—	1
Passeriformes indet.		1	—	2	—	3
Aves indet.		7	19	118	22	166
NISP total		13 (6)	28 (9)	157 (39)	38 (16)	236 (70)

some other fossil assemblages at Olduvai. Tooth marks are small and were likely made by smaller carnivores such as mongoose, genet, jackal or serval, based on my direct observations of carnivore feeding episodes. Fossil wing bone specimens are both less weathered and less likely to be tooth-marked than leg specimens. Similar patterns of weathering (Prassack, in press) and carnivore damage (pers. obs.) have been observed in modern settings and suggest a link between these taphonomic agents and skeletal part bias, at least for the preferential survivorship of wings over legs.

Wetland Interior (FLK NN). The northernmost deposits in the FLK Complex are reconstructed as perennial wetlands based on the presence of extensive marsh plant mats consisting of *Typha* and *Phragmites* macrofossils on the surface of an olive waxy claystone, indicative of a previous lake inundation of the area (Blumenschine *et al*., in press).

The Leakey excavations at FLK NN (Levels 1–4) recovered over 3,000 specimens representing a range of avifauna. It is unknown what the actual numbers are for Level 1, but Matthiesen (1990) notes that shorebirds dominate, followed by ducks and rails, supporting the presence of wetlands, emergent vegetation and standing water. The much smaller OLAPP assemblage at FLK NN is not surprisingly much less diverse, predominately represented by small shorebirds, including examples of medullary bone suggesting that Lake Olduvai was a breeding ground for some shorebirds. Mourning Dove (*Streptopelia decipiens*) is not unexpected since these birds rely of fresh water for drinking and bathing and their carcasses have been observed along the edges of freshwater pools and saline-alkaline lake flats. The absence of typical wetland taxa (e.g., ducks, herons, rails) in OLAPP's assemblages is most likely an artifact of sample size (NISP =157). Alternatively though not determinable with this small sample, it attests to the patchiness of near-shore landscapes.

Two of the wetland interior trenches (145 and 134) are located on what appears to have been a small topo-high. No birds were recovered from Trench 134, and specimens from Trench 145 exhibit slightly heavier fragmentation and weathering than bones at Trench 135, which is hypothesized as deep marsh. This suggests prolonged exposure on the surface of the mound rather than quick burial. KAP has observed Blacksmith Plover (*Vanellus armatus*) carcasses lying atop clumps of sedge grass (*Cyperus laevigatus*) in near-shore, spring-fed wetlands at Lake Manyara, Tanzania (Prassack, unpublished). Clumping or a general lack of vegetation on the Wetland Interior topo-high may have left bone exposed to more prolonged subaerial weathering.

Table 2. Raw data and percentages for weathering and incidence of carnivore tooth markings, rodent gnawing, trampling, and microbial bioerosion across the *Zinjanthropus* equivalent landscape. Weathering and carnivore tooth-marks for wing and leg elements are emphasized. In parentheses are percentages for a given column. Note: Ten specimens from the Wetland Edge were not analyzed because they were small (< 5 mm) mid shaft fragments. This lowered the total assemblage size to 226, which is reflected in percentages for the Wetland Edge and FLK Complex totals for rodent gnawing, trampling, and bioerosion. It does not affect wing and leg percentages.

landscape facet	Channel	Peninsula	Wetland		FLK Complex
			Edge	Interior	
taphonomic trace	FLKS	FLK	FLKN	FLKNN	total
wing : leg ratio	3:1 (75)	10:4 (71.4)	60:34 (64.5)	15:7 (68.2)	88:46 (66.2)
WS 0-1					
all elements	7 (53.8)	20 (71.4)	107 (72.7)	29 (76.3)	163 (72)
wings	0 (N/A)	3 (75)	22 (64.7)	7 (100)	30 (65.2)
legs	1 (7.1)	11 (39.3)	40 (27.2)	9 (23.7)	61 (25.8)
tooth-marked					
all elements	1 (7.7)	11 (39.3)	40 (27.2)	9 (23.7)	61 (27.0)
wings	0 (N/A)	6 (60)	15 (25)	2 (13.3)	23 (26.1)
legs	0 (N/A)	2 (50)	14 (41.1)	2 (28.6)	18 (39.1)
rodent-gnawed	1 (7.7)	4 (14.3)	13 (8.9)	0 (N/A)	18 (7.6)
trample-marked	1 (7.7)	3 (10.7)	5 (7.3)	2 (5.2)	11 (4.9)
bioerosion	3 (23.1)	8 (28.6)	11 (5.2)	2 (7.5)	24 (10.0)

Tooth-marked bird bones in this facet suggest only moderate damage by carnivores, although there is a dominance of wing bones. Conversely, the larger mammal assemblage shows a stronger, larger-carnivore signal in the form of low bone densities, an absence of limb bone ends, and many tooth-marked bones (*cf.* Blumenschine, 1995; Blumenschine *et al.*, in press).

Wetland Edge (FLK N). OLAPP reconstructs this facet as the edge of a perennial wetland abutting the topographically higher Peninsula to the south. A range of *in situ* sedge culms and stems of dicots are present, plus woody stems and branches, the latter of which were likely washed down slope from the Peninsula. Crocodiles and the presence of grebes and teals support proximity to open water while the rails and the small heron imply wetlands and emergent vegetation with sufficient cover. The ecotonal nature of this facet is evident from the occurrence of dove, mousebird, and lovebird, which implies trees or bushes in the vicinity, as also evidenced for the adjacent Peninsula facet. These brush/woodland birds likely utilized small pools of water at the Wetland Edge to drink and bathe, as is seen today at the Cheetah Marsh at Lake Ndutu, Tanzania (pers. obs.). This behavior may have exposed them to greater predation risk. The Wetland Edge provides the highest densities of fossil birds from the FLK Complex but this may be an artifact of screening methods since it was only for these trenches that wet/dry sorting was done. Low overall weathering supports this as an area with either sufficient vegetative ground cover and/or quick burial. The absence of skeletal remains of larger wetland birds (e.g., pelicans, geese, stork), commonly encountered in similar modern landscape settings, may be the result of water-logged cracking, where water is repeatedly leached from exposed drying bone (Trueman *et al.*, 2003; Prassack, in press). This is expected to occur, and has been observed by KAP along wetland edges that dry out along their outer margins seasonally. This phenomenon may have a greater affect on larger bones that may remain unburied and exposed on the surface longer than smaller bird bones (pers. obs.). Small carnivore activity, as seen in the incidence of tooth marking, is moderate compared to the other assemblages. In contrast, the larger carnivore signal on larger mammal specimens is low, with high survivorship of large mammal limb bone ends and few tooth-marked specimens occurring (Blumenschine *et al.*, in press). However, crocodile tooth marks occur on several large mammal bones and the high number of complete larger mammal bones in this facet is indicative of crocodile feeding (Njau & Blumenschine, 2006). Rodent gnawing lends further support of adequate vegetation that would have concealed rodents from aerial predators.

Peninsula (FLK). OLAPP excavations identify the presence of a patchily-treed narrow peninsula that rose approximately 0.5 to 1 m above the Wetland Complex to its north and the River Channel to its southeast (Blumenschine *et al.*, in press). Trees are inferred along its southern face, based on high densities of micro-mammal remains from FLK Level 22 (Fernandez-Jalvo *et al.*, 1998) and what has been inferred to be a depression created by an uprooted tree (M.D. Leakey, 1971). High densities of siliceous roots and their casts, in addition to grasses and sedges, are present, but an absence of micro-mammals and woody vegetation at Trench 138 are suggestive of open grassy habitat along part of the Peninsula facet (Blumenschine *et al.*, in press).

Mary Leakey's massive excavation at FLK produced dense concentrations of stone tools and vertebrate fossils, including cut-marked larger mammal bones, leading her and others to describe Level 22 as a hominid living site or home base (M.D. Leakey, 1971; Bunn, 1981; Potts, 1984). Many bones, however, are also tooth-marked by large carnivores and/or crocodiles (Njau & Blumenschine, 2006), suggesting heavy competition for carcass-scavenging and high predation risk to hominids. Carnivore tooth-marked larger mammal bone is abundant at Level 22 (Blumenschine, 1995), but uncommon elsewhere on the Peninsula (Blumenschine *et al.*, in press).

Over 2,000 avifaunal specimens were recovered from Level 22 by the Leakeys (Matthiesen, 1990). As at FLK NN, shorebirds, ducks and rails dominate but cormorants (Brodkorb & Mourer-Chauviré, 1984) and raptorial birds (Matthiesen, 1990) are also present, suggesting the presence of roosting trees or rocky outcrops in the vicinity. OLAPP trenches produced far fewer specimens but with moderate species diversity and excellent preservation allowing for 32% of specimens to be identified to family or genus (e.g., ducks, rails, several larger sandpipers, a dove and a small corvid).

A higher proportion of bird bones bear small carnivore tooth marks in this part of the complex. Carnivores commonly remove carcasses from open ground, as would be expected along a marsh edge, to areas to cover (i.e., a treed peninsula with a brush slope) to reduce kleptoparasitism risk from other carnivores. Allen's Gallinule (*Porphyrio alleni*) and the ducks might have been brought in from the adjacent wetland by a carnivore or the ducks may have fallen victim while nesting in the tall grass along the peninsula. This is supported by the presence of tooth marks on specimens of Common Teal (*Anas crecca*) and of *Aythya* sp. The higher ground of the Peninsula would have also provided a clearer view of danger. Accumulations of tooth-marked bird bone have been observed at the Ngorongoro Burial Mounds, a series of lightly vegetated hills ranging in size between 50 and 400 m and elevations as high as 50 m spread along ca. 2.5 km of an otherwise low grade, upper lacustrine plain in the Ngorongoro Crater of Tanzania. Those remains include Yellow-necked Spurfowl (*Francolinus leucoscepus*), which are expected along the upper grassy plains, but also pelican, which was likely transported from freshwater springs or the lake shore approximately 1 km away. Rodent gnawing is most common in this facet and correlates to the abundance of micromammal remains recovered at FLK (Fernandez-Jalvo *et al.*, 1998; Blumenschine *et al.*, in press).

Etching by filamentous fungi (Fernandez-Jalvo *et al.*, 2002) and dendritic-patterned staining by manganese dioxide are common here and suggest a dry, low-light area where lichen is typically found (Fernandez-Jalvo *et al.*, 2002; Thackery *et al.*, 2005). Trample-marked bone at Trench 140 suggests an exposed high-traffic area with some cover, on a gritty sandy substrate (Fiorillo, 1989), as would expected in an area between two freshwater sources.

Channel/Spillway (FLK S). An anastomising river flowed parallel to the Peninsula in the area of FLK S (Blumenschine *et al.*, in press). It was likely seasonal, as are many in the Rift Valley. Botanical data are limited to silicified rhizomes believed to be perennial sedges, which are common along river banks today. Larger mammal bone densities are low here, limb bone ends are absent, and carnivore tooth marked bones are found on 50% of larger mammal bones, suggesting that this, along with the Wetland Interior, were areas of heavy larger carnivore activity. The Peninsula likely provided shade along the northern banks of the River Channel, and lions, leopards, and hyenas frequent riverine habitats today to both hunt and rest, producing common kill-site bone assemblages along river banks in East Africa (pers. obs.).

Bird bone densities are also low here. Many larger birds (vulture, eagle, crowned crane) congregate at rivers to bathe, but African water birds prefer standing water (O'Keefe, 1986), and the flow of this river, while likely seasonal, may alone have been of sufficient velocity to restrict or limit avian activity. Surveys in modern landscape facets of Tanzania (Prassack, in prep.) yielded few avian remains in riverine settings at Lake Manyara and Ngorongoro Crater but strong evidence of carnivore activity, including scat, prints, hair balls, as well as hyena, jackal and lions resting in the shade along the banks. The small avifauna sample size makes it difficult to discuss this facet's taphonomy, but based on modern observations one can expect that high carnivore activity and fluvial transport, coupled with exposure to subaerial weathering, will result in low survivorship potential for bird bones in riverine environments.

Application to study of hominid land use at Olduvai. The Olduvai fossil birds provide additional supporting evidence of paleolandscape structure and ecology in the FLK Complex during Middle Bed I times, as well as novel environmental information lacking from other biotic proxies. For example, the proximity of the lake to the complex cannot be currently defined, but the abundance of small shorebirds (plovers and sandpipers) in the wetland interior suggests near shore environments and close proximity to mudflats. The presence of shorebird medullary bone implies that Olduvai was a breeding ground for at least some taxa. Diving birds (cormorant, teal and grebe) attest to lake depth, and marsh birds (moorhen, crake, swamphen, and flufftail) suggest suitable emergent vegetation, which is further supported by the paleobotanical evidence. Geomorphic data point to dry, higher ground in the area of FLK, which we interpret as a peninsula, and are directly supported by the occurrence of various perching and bush/grassland birds including the likelihood of nesting cormorants and predatory bird roosts.

The taphonomic analysis, even of specimens that could not be described beyond Aves or to skeletal element (i.e., midshaft fragments), provides additional data supporting OLAPP's landscape reconstructions. Weathering is lowest in the Wetland Interior where bones likely become mired in mud and are unaffected by solar radiation. Damage by carnivores is highest at the Peninsula, where they would have had sufficient access to cover as well as to birds nesting, drinking and/or bathing in nearby freshwater pools of the Wetland Edge. Rodent damage and trampling, while not common, also correlate to landscape facet, with rodent gnawing occurring in areas of adequate ground cover (Peninsula and Wetland Edge) and trampling along the Peninsula, where herds of large mammals would be expected to frequent. The bioerosion, while treated here anecdotally, does show similarities to modifications and staining seen in some modern habitats, justifying further study.

With these data, hominid land use patterns can be better ascertained. Hominids likely avoided much of the Wetland Interior owing to its inaccessibility and dangers from crocodiles, hippopotamus and larger mammalian carnivores. This is evident in the absence of stone tools or cut-marked mammal bones in the facet (Blumenschine *et al.*, in press). Hominids may have accessed the Wetland Edge to harvest rootstocks, acquire large mammal carcasses left by carnivores, and to gather bird eggs and nestlings. The adjacent, treed Peninsula would have provided nearby arboreal refuge for hominids to escape terrestrial predators, and could have served as relatively safe foci for processing carcasses brought in from the nearby Wetland and Channel. The Peninsula may also have afforded hominids access to various fruiting trees lining the banks of abandoned channels crossing this facet. Such a reconstruction could explain the strong evidence of hominid activity, including the abundant stone tools and cut-marked mammal bones seen here. We did not find nor did we expect cut-marked bird bones, but if hominids were indeed processing larger bird carcasses, it is in facets such as the Peninsula that we would expect to find evidence. However, large carnivores frequent river banks in search of prey, and buffalo and elephant can be found traversing dried river banks (Prassack, pers. obs.), making this an unlikely place for prolonged hominid activity such as that imagined in the living-site scenario. This is attested to by evidence of mammalian carnivore and crocodilian tooth marks on hominid bones recovered from the Peninsula (Blumenschine *et al.*, in press).

Conclusion

A relatively small avifaunal assemblage (NISP = 236) is shown to corroborate and strengthen OLAPP reconstructions of the paleolandscapes at the FLK Complex during the Late Pliocene. Our results support previous claims that fossil birds (Baird, 1989; Cheneval, 1989), even small assemblages (Behrensmeyer *et al.*, 2003), can provide important paleoenvironmental data, particularly when recovered as part of an excavated landscape sample. In this instance we are better able to delineate hominid land use strategies as these relate to their subsistence and exposure to competition and predation hazards. The taphonomy of these fossils also proves useful for understanding site paleoecology and landscape distribution by providing fine scale detail on microhabitat and landscape heterogeneity that may not be apparent through the analysis of other proxies (e.g., mammalian fauna, botanical and sedimentological samples). These findings should encourage others to include avifaunal remains when studying site taphonomy but also promote the continuation of modern analogue studies across a wider range of depositional environments in order to increase the validity of taphonomic-based reconstructions at fossil sites. Earlier reports by Hay (1976), Brodkorb (1980), and Matthiesen (1990), coupled with the results from this study, suggest that the Olduvai birds will play an increasingly significant role in the understanding of Plio-Pleistocene avifaunas in Africa.

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Avifaunal Responses to Warm Climate: The Message from Last Interglacial Faunas

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ABSTRACT. The possible effect on avifaunas of a hypothetical future warmer climate has recently caused much speculation, frequently ill-founded. On the other hand the actual effects of past warmer interglacials on avifaunas have strangely enough attracted no interest. This paper is an effort to remedy this, by reviewing the avifaunas of the previous interglacial (MIS 5e, 117–130 Ka BP). This interglacial was significantly warmer than the present one, about 2°C in the North Temperate zone and 5°C or more in the Arctic, and may have been the warmest interval since the Pliocene. Most of the known Last Interglacial avifaunas are from the temperate parts of North America and Europe. The scarcity of avifaunas from other areas are due both to a scarcity of Pleistocene avifaunas in general and to rudimentary Quaternary chronologies, which makes it difficult to date faunas older than the last glaciation. In North America, the largest collections are from California and Florida. The Californian faunas are similar to modern faunas, both for seabirds and landbirds, while the Florida faunas contain a number of extralimital Central American and South American species. A small fauna from Arctic Canada (Old Crow Basin) is also similar to modern faunas. In Europe, several faunas from Central Europe differ little from extant faunas in the same areas, while faunas from Great Britain contain some southern (Iberian) species. Material from the southern hemisphere is very limited, and consists of one small fauna from New Zealand which is similar to modern faunas from the same area. The only LIG avifauna that shows dramatic differences from present-day conditions is from southwestern Egypt. This area is now extreme desert but had a rich Afrotropical avifauna during LIG, presumably due to a northward expansion of the African Monsoon. In general it seems that a temperature rise of the order of 2°C does not have a very dramatic impact on temperate avifaunas, while in the tropics changes in precipitation patterns may be more important than temperatures.

TYRBERG, TOMMY, 2010. Avifaunal responses to warm climate: the message from Last Interglacial faunas. In *Proceedings of the VII International Meeting of the Society of Avian Paleontology and Evolution*, ed. W.E. Boles and T.H. Worthy. *Records of the Australian Museum* 62(1): 193–205.

The possible effect on avifaunas of a hypothetical future warmer climate has recently caused much speculation However the actual fossil data on avifaunas during past warmer interglacials have attracted very little or no interest. This paper is an effort to address this oversight.

The last interglacial (MIS 5e, about 130–117,000 years BP) is of special interest in this context. It was apparently about 2°C warmer than modern climates globally and up to 10°C warmer in large parts of the Arctic (e.g., Velichko *et al.*, 2008, CAPE-Last Interglacial Project Members, 2006), while sea-levels were a few meters higher than at present, though the exact figure is very uncertain. As a matter of fact to judge from the δ^{18}O record MIS 5e was the warmest interval since the Pliocene (ca. 2.5 Ma), and to find a sustained period of lower δ^{18}O one has to go back about 4 million years to the Early Pliocene warm period (Lisiecki & Raymo, 2005).

Because the last interglacial *sensu stricto* (i.e. MIS 5e) is known by a variety of local names (Sangamonian, Eemian etc.) the term Last Interglacial (LIG) will be used in this paper.

In general, fully interglacial avifaunas are disproportionally rare compared to faunas from colder intervals, particularly in cave environments. The reason for this is not well understood.

The LIG has a much better avifaunal record than the two preceding interglacials with approximately equal peak temperatures (MIS 9 and 11) but even so, avifaunas which are securely dated to the LIG and are diverse enough for meaningful paleoecological studies are unfortunately almost exclusively available from North America, Europe and northern Africa. Only a single small fauna is known from the southern hemisphere (Table 9).

This geographical limitation is to a large extent due to the fact that in most parts of the World dating of Pleistocene faunas to specific glaciations or interglacials is not yet possible beyond the range of C14 dating.

Methods

To study the effect of climate on the avifaunas the arealogram method (Grichuk, 1969, 1984) was used. This is done by superimposing the modern ranges of all the species in the fossil fauna. The area where all species coexist today defines their common range and the range of environments acceptable to all the species.

If there is no area where all the species of the fossil fauna occur together today, this may either indicate that the environmental conditions have no exact modern counterpart, that the modern range of some of the species have been modified by human action, or that the ecological requirements of some of the species have changed since the LIG. The latter possibility is difficult to evaluate, but seems unlikely to be important over such a relatively short period (ca. 100,000 years).

This method has been much used for plants, including LIG floras (see for example Velichko *et al.* [2008] and references cited therein) and also for mammals, but rarely for birds, probably because of their great mobility (e.g., Harris, 1985). For migrant birds it is moreover necessary to include both wintering areas and areas through which they migrate, unless breeding can be proven by the presence of unfledged juveniles or individuals with medullary bone.

No extinct species have been used in the analysis, since their modern range is not obtainable. Only determinations regarded as secure were used in the analysis. In some cases determinations to genus, e.g., *Cygnus* sp., have been used. In such cases the total range of all species in the genus were used. A further restriction in such cases is that no extinct species belonging to the genus must be known from the applicable area and time interval.

The following sources have been used for range data: North America—The Birds of North America (BNA) (http://bna.birds.cornell.edu/bna/), and Price *et al.*, (1995). Europe—Cramp *et al.* (1977–1994), and Hagemeijer & Blair (1997). Africa—Sinclair & Ryan (2003), and Moreau (1972). New Zealand—P. Harrison (1983). Nomenclature and the species order follow Clements (2007). For extinct taxa not found in Clements the nomenclature follows Tyrberg (2008, 2009).

Results

North America. In North America extensive LIG avifaunas are known from southern California and central Florida, with only a few sites from other parts of the continent (Fig. 1).

Los Angeles basin. The LIG climate in southern California is relatively well known from studies of marine deposits. Offshore sea-surface temperatures may have been as much as 3°C warmer than at present while coastal faunas indicate temperatures only slightly higher than today (Muhs *et al.*, 2002, 2006). This is in accord with palynological evidence about the coastal flora which also indicate temperatures similar to or slightly warmer than at present (Heusser, 2000).

The avifaunas from the Los Angeles basin in southern California derive from more than a dozen sites in the LIG marine Palos Verdes Sand (Table 1). Most, if not all, avian remains derive from the "fossil hash" bed. This is an event bed, possibly a tsunamite (Jacobs, Marks & Brown, 2001), which means that the emplacement of the layer was geologically instantaneous though it may of course incorporate older deposits. There seems to be no definite information on the stratigraphic position of this bed within the LIG. This fauna is unusual because while it consists mostly of an exceptionally rich seabird fauna, it also has an appreciable landbird component, probably as a result of its unusual mode of deposition. This makes it possible to analyze conditions both in the sea and on land at the time of deposition.

The composite fauna from the sites in Table 1 consists of 48 analyzable taxa, of which 28 are analyzable as marine or coastal and 20 as land-birds. *Phoebastria albatrus* was not used, since it is now so rare as a result of excessive hunting that its range can not be determined, though it seems to have been the most common albatross in the area during the LIG. Both subfaunas are very similar to the modern avifauna of southern California. The co-occurrence area for the landbirds is a very limited area in the central San Joaquin Valley and the one for the seabirds a short stretch of coast

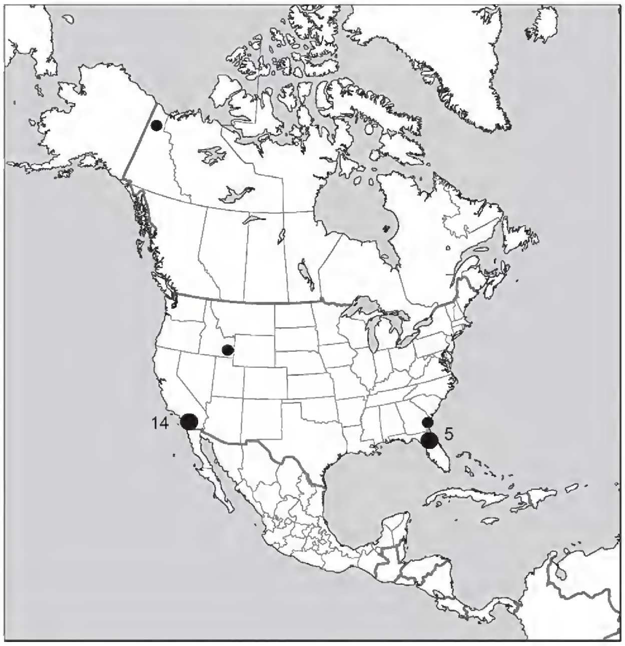

Figure 1. Sites with Last Interglacial avifaunas in North America.

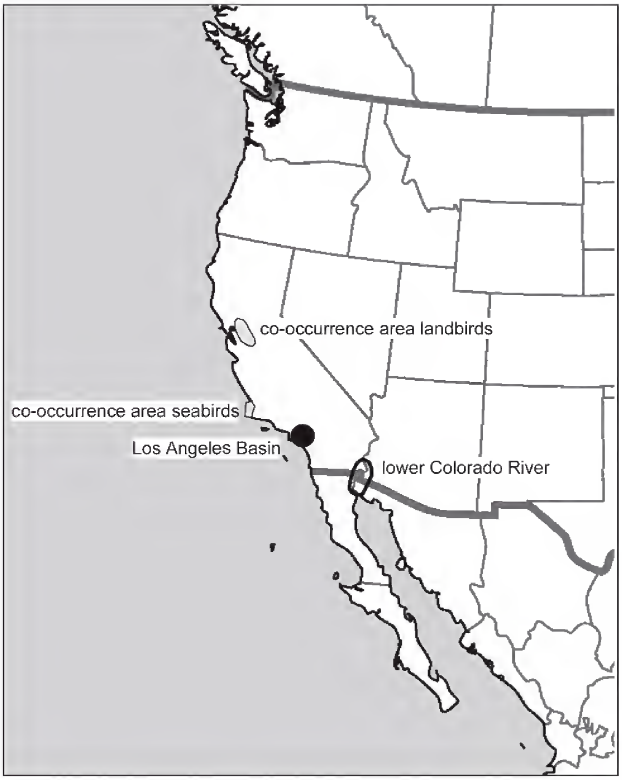

Figure 2. Modern co-occurrence for LIG seabird and landbird faunas from the Los Angeles Basin (shaded areas). The unshaded area on the lower Colorado River marks an area where 19 out of 20 landbirds occur.

in the Lompoc area just northwest of the Los Angeles Basin (Fig. 2). However all landbirds except one also occur along the lower Colorado River 200 km east of the Los Angeles Basin. The species that do not occur in the Los Angeles Basin today are almost exclusively dependent on wetlands or wet meadows, so the avifaunas suggest temperatures similar to the present both on land and in the sea, but with more wetlands than at present.

Florida

The LIG climate of Florida is not well understood due to a paucity of securely dated organic deposits. However the Florida climate is very much determined by the surrounding ocean, and sea-surface temperatures are known to have been similar to or slightly warmer than at present (Muhs *et al.*, 2002) and this is supported by the limited data available on terrestrial vegetation (e.g., Heusser & Oppo, 2003). The maritime influence would presumably have been even stronger than today since sea-level was slightly higher than at present, and southern Florida (south of the present Lake Okeechobee) was a shallow marine/mangrove habitat similar to the modern Florida Bay. To the west along the Gulf coast limited pollen data from LIG beach barrier complexes indicate vegetation similar to modern conditions (Otvos, 2005).

There are a total of seven LIG sites with avifaunas known from central Florida, of which two (Haile VIIA and VIIIA) contain, respectively, only *Meleagris* and *Coragyps atratus*, so are not included in the analysis (Table 2). In contrast to other areas the Florida LIG avifaunas are largely derived from karstic sites (sinkholes). In all the faunas comprise 104 taxa, of which 7 are extinct. The largest fauna is from Haile XIB with 64 analyzable taxa. Of these, the maximum number of co-occurring taxa at the present time comprises 58 taxa along the upper Texas coast and 56 taxa in south-central Florida (Fig. 3).

The results for the other sites are similar. Rock Springs, with 36 species has all species co-occurring in northern Florida including around the find locality (Fig. 4). Arredondo IIA with 29 analyzable species has a larger area of maximum co-occurrence with 27 species occurring in central and northern Florida and in a coastal belt from Texas to South Carolina (Fig. 5) while Reddick IB/D has 18 from a total of 23 analyzable species co-occurring in a very similar area (Fig. 6). The odd one out in this group is Arredondo IA with 12 species and with two areas of maximum co-occurrence of 11 species each, one in central Florida and one in the mountains of northern Virginia and Maryland (Fig. 7). This strange distribution is due to the presence of *Bonasa umbellus* in the fauna. There is some evidence that *Tsuga* was more widely distributed in southeastern North America during the LIG than during the Holocene (Heusser & Oppo, 2003), but even so it seems unlikely that *Bonasa umbellus* would have occurred in Florida under fully interglacial conditions. It seems more likely that the Arredondo IA fauna is misdated and actually dates at least in part from one of the late cool phases of MIS 5 (i.e. MIS 5b or 5d).

Since the areas of maximum modern co-occurrence (except for Arredondo IA as noted above) are close to or overlap the fossil sites the extralimital species are of particular interest for determining deviations from current environmental conditions.

The extralimital species mostly fall into three groups:

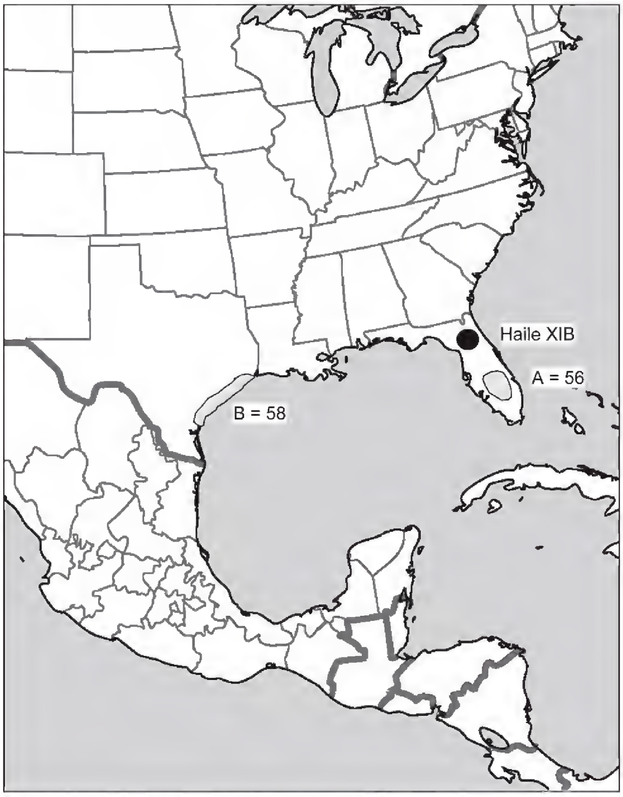

Figure 3. Modern areas of maximum co-occurrence for the Haile XIB avifauna (64 analyzable taxa).

Table 1. Last Interglacial (LIG) faunas from Palos Verdes Sands localities in the Los Angeles basin. Extinct taxa are indicated by a †. (1) Bixby slough, Harbor City; (2) Chandler Sand Pit, Rolling Hills Estate; (3) Hill 48, San Pedro Lumber Company, San Pedro; (4) Lincoln Avenue, Playa Del Rey; (5) Long Wharf Canyon, Santa Monica; (6) Naval Fuel Reserve Quarry, Harbor City; (7) Naval Housing Unit, Harbor City; (8) Pacific Avenue and Oliver Street, San Pedro; (9) Pacific Avenue and Second Street, San Pedro; (10) United States Veterans Hospital, Long Beach; (11) Gen. MacArthur Blvd., Newport Bay Mesa, Newport Beach; (12) Newport Bay Mesa, Loc. 1066, Newport Beach; (13) Newport Bay Mesa, Loc. 1067, Newport Beach; (14) Orizaba and Second Street, San Pedro. Sources: Brodkorb (1964, 1967), Howard (1936, 1944, 1947, 1949, 1955, 1958), Jefferson (1991), Langenwalter (1975), L.H. Miller (1914, 1925, 1930), W.E. Miller (1971), Miller & DeMay (1942). ● = present; ●? = doubtfully present; — = not present.

species	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Anser albifrons	—	—	●	—	—	—	—	—	—	—	—	●	—	—
Chen caerulescens	—	—	—	—	—	—	●	—	—	—	—	—	—	—
Branta bernicla	—	—	cf	—	—	—	—	—	—	—	—	—	—	—
Branta canadensis	—	—	●	—	—	—	●	—	—	—	—	●	—	—
Anas americana	—	—	●	—	—	—	—	—	—	—	—	—	—	—
Anas platyrhynchos	—	—	●	—	—	—	—	—	—	—	—	—	—	—
Anas clypeata	—	—	●	—	—	—	—	—	—	—	—	—	—	—
Anas [crecca] carolinensis	—	—	●	—	—	—	—	—	—	—	—	—	—	—
Anas sp.	—	—	—	●	—	●	—	—	—	—	—	—	—	—
Aythya valisneria	—	—	—	—	—	—	—	—	—	—	—	●?	—	—
Aythya affinis	—	—	—	—	—	—	—	—	—	—	—	—	cf	—
Melanitta perspicillata	—	—	●	—	—	—	—	—	—	—	—	—	—	—
Melanitta fusca	—	—	●	—	—	—	—	—	—	—	—	●?	—	—
† *Chendytes lawi*	●	●	●	●	●	—	—	—	●	●	sp.	●	—	—
Bucephala albeola	—	—	●	—	—	—	●	—	—	—	—	—	—	—
Callipepla californica	—	—	●	—	—	—	—	—	—	—	—	—	—	●
Callipepla sp.	—	—	—	—	—	—	—	—	—	—	—	—	●	—
Galliformes sp.	—	—	—	—	—	—	●	—	—	—	—	—	—	—
Gavia stellata	—	—	—	—	—	—	—	—	—	—	—	●	—	—
Gavia pacifica	—	—	●	—	—	—	—	—	—	—	—	—	—	—
Gavia immer	—	—	●	aff.	—	—	—	—	—	—	—	●	—	—
Gavia sp.	—	●	—	—	—	—	—	—	—	●	—	—	—	—
Podiceps auritus	—	—	cf	—	—	—	—	—	—	—	—	—	—	—
Podiceps nigricollis	—	—	●	—	—	—	—	—	—	—	—	—	—	—
Aechmophorus occidentalis	—	●	—	●	—	—	—	—	—	—	—	●?	—	—
Phoebastria nigripes	—	—	●	—	—	—	—	—	—	—	—	—	—	—
Phoebastria albatrus	—	—	●	●	—	—	—	—	—	—	—	●	—	—
Phoebastria sp.	—	—	●	—	—	—	—	—	—	—	—	—	—	—
Fulmarus glacialis	—	—	●	—	—	—	—	—	—	—	—	●	—	—
Puffinus griseus	—	—	●	●	—	—	—	●	—	—	—	●	—	—
Puffinus opisthomelas	—	—	●	●	—	—	—	—	—	—	—	●?	—	—
† *Morus reyana*	—	—	—	●	—	—	—	—	—	—	—	●	—	—
Pelecanus sp.	—	—	—	—	—	●	—	—	—	—	—	—	—	—
Phalacrocorax penicillatus	—	—	●	—	—	—	—	—	—	—	—	●	—	—
Phalacrocorax auritus	—	—	●	—	●	—	—	—	—	—	—	—	—	—
Phalacrocorax sp.	—	—	—	—	—	●	—	—	—	—	—	—	—	—
Coragyps sp.	—	—	●	—	—	—	—	—	—	—	—	—	—	—
Cathartes aura	—	—	●	—	—	—	—	—	—	—	—	—	—	—
Haliaeetus leucocephalus	—	—	●	—	—	—	—	—	—	—	—	—	—	—
Accipiter sp.	—	—	—	—	—	—	—	—	—	—	—	—	●	—
Falco sparverius	—	—	●	—	—	—	—	—	—	—	—	—	—	—
Fulica americana	—	—	●	—	—	—	—	—	—	—	—	—	—	—
Tringa semipalmata	—	—	—	—	—	—	—	—	—	—	—	●	—	—
Tringa sp.	—	—	●	—	—	—	—	—	—	—	—	—	—	—
Limosa fedoa	—	—	cf	—	—	—	—	—	—	—	—	—	—	—
Larus glaucescens	—	—	●	—	—	—	—	—	—	—	—	—	—	—
Larus sp.	—	—	—	—	—	—	—	—	—	—	—	●	—	—
Stercorarius sp.	—	—	—	—	—	—	—	—	—	—	—	●	—	—
Uria aalge	—	—	—	●	—	—	—	—	—	—	—	—	—	—
Synthliboramphus antiquus	—	—	●	—	—	—	—	—	—	—	—	—	—	—
Ptychoramphus aleuticus	—	—	●	—	—	—	—	—	—	—	—	—	—	—
Passeriformes sp.	—	—	—	—	—	—	●	—	—	—	—	—	—	—
Corvus corax	—	—	—	●	—	—	—	—	—	—	—	—	—	—
Corvus sp.	—	—	—	—	—	—	—	—	—	—	—	—	●	—
Agelaius phoeniceus	—	—	—	—	—	—	—	—	—	—	—	—	●	—
Sturnella neglecta	—	—	●	—	—	—	—	—	—	—	—	—	—	—

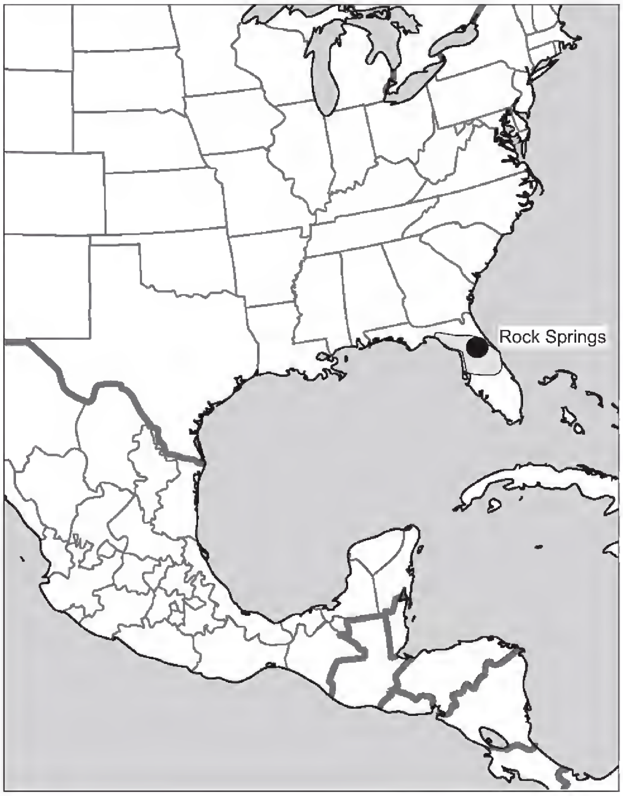

Figure 4. Modern areas of co-occurrence for the Rock Spring avifauna (36 analyzable taxa).

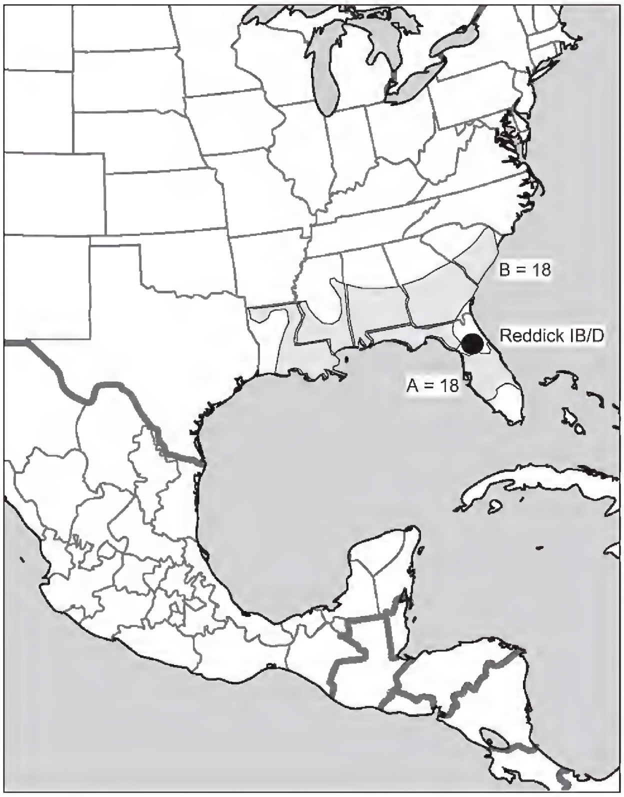

Figure 6. Modern area of maximum co-occurrence for the Reddick IB/D avifauna (23 analyzable taxa).

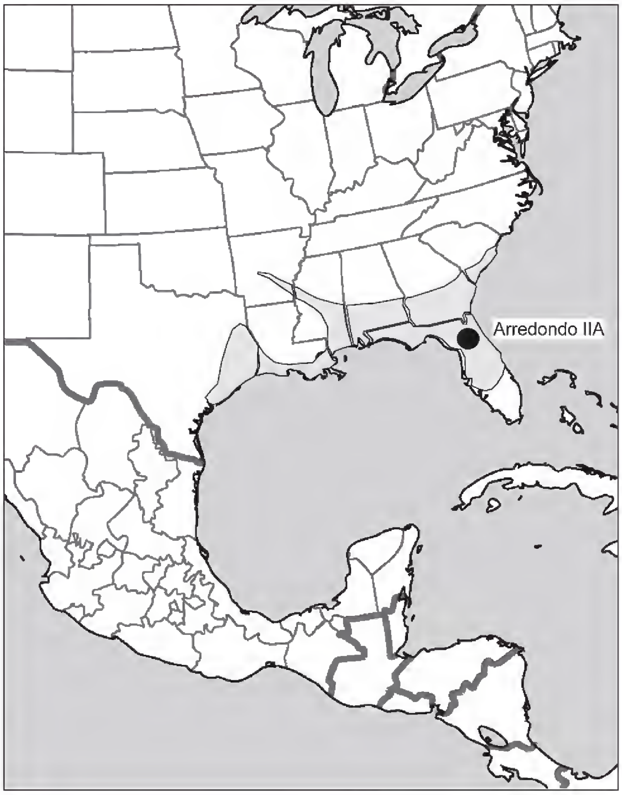

Figure 5. Modern area of maximum co-occurrence for the Arredondo IIA avifauna (29 analyzable taxa).

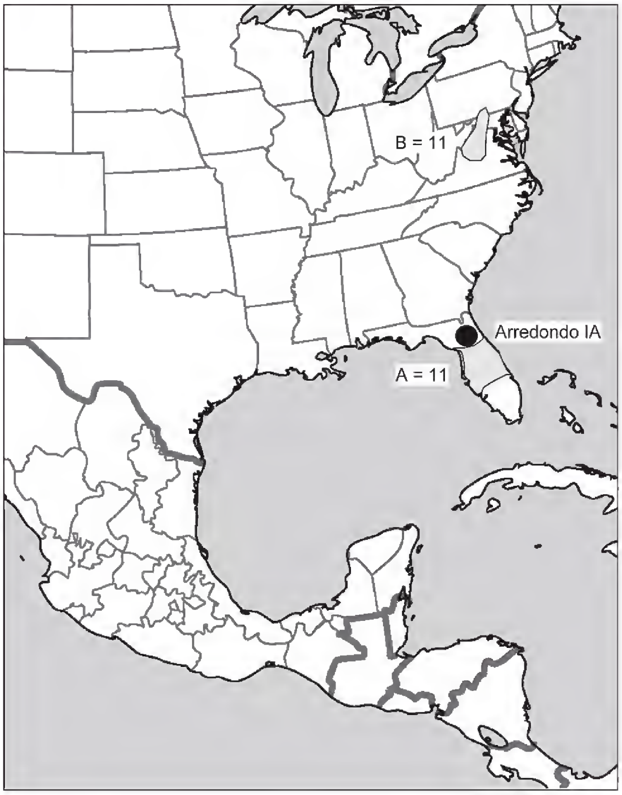

Figure 7. Modern areas of maximum co-occurrence for the Arredondo IA avifauna (12 analyzable taxa).

Table 2. Last Interglacial (LIG) faunas from localities in central Florida. Extinct taxa are indicated by a †. List of localities: (1) Haile XIB; (2) Rock Spring; (3) Arredondo IA; (4) Arredondo IIA; (5) Reddick 1B–D. Sources: Brewer (1969); Brodkorb (1957, 1959, 1967, 1978); Emslie (1998); Frailey (1972); Hamon (1964); Holman (1961); Ligon (1965); Olson (1974); Steadman (1976, 1980); Woolfenden (1959). Florida Museum of Natural History Collection database.

	species	1	2	3	4	5
	Branta canadensis	●	—	—	—	—
	Aix sponsa	●	●	—	—	—
	Anas platyrhynchos	●	—	—	—	—
	Anas fulvigula	—	●	—	—	—
	Anas discors	●	●	—	●	—
	Anas clypeata	●	—	—	●	—
	Anas acuta	●	●	—	—	—
	Anas [crecca] carolinensis	●	●	—	●	—
	Anas sp.	—	●	—	—	—
	Aythya collaris	●	●	●	—	—
	Aythya affinis	●	●	—	—	—
	Clangula hyemalis	●	—	—	—	—
	Bucephala albeola	●	—	—	—	—
	Lophodytes cucullatus	●	—	—	●	—
	Mergus serrator	—	●	—	—	—
	Bonasa umbellus	—	—	●	—	—
	Tympanuchus cupido	●	—	—	—	—
	Meleagris gallopavo	—	cf	●	●	cf
	Colinus virginianus suilium	●	—	●	●	●
†	*Neortyx peninsularis*	●	—	—	—	—
	Gavia immer	—	●	—	—	—
	Podilymbus podiceps	●	●	●	●	—
	Podiceps auritus	—	●	—	—	—
	Phalacrocorax auritus	—	●	—	—	—
	Anhinga anhinga	—	●	—	—	—
	Botaurus lentiginosus	●	●	—	—	—
	Ardea herodias	—	●	—	—	—
	Ardea alba	—	●	—	—	—
	Egretta thula	●	—	—	—	—
	Butorides virescens	●	—	—	—	—
	Nycticorax nycticorax	—	●	—	—	—
	Platalea ajaja	—	●	—	—	—
†	*Ciconia maltha*	—	●	—	—	—
	Coragyps atratus	—	●	—	—	—
(†)	*Coragyps [atratus] occidentalis*	—	●	—	—	●
	Gymnogyps californianus amplus	—	—	—	—	●
	Cathartidae sp.	—	—	—	—	●
	Pandion haliaetus	—	●	—	—	—
	Ictinia mississippiensis	—	—	—	—	●
	Haliaaetus leucocephalus	—	●	—	—	—
	Accipiter cooperii	●	—	●	—	—
	Buteo platypterus	●	—	—	—	—
	Buteo jamaicensis	—	●	●	—	—
	Caracara cheriway plancus	●	—	—	—	—
	Milvago chimachima readei	—	—	—	●	●
	Falco sparverius	●	—	—	●	—
	Falco peregrinus	●	—	—	●	—
	Coturnicops noveboracensis	●	—	—	—	—
	Laterallus exilis	●	—	—	—	●
	Rallus elegans	●	—	—	●	—
	Rallus limicola	●	—	—	●	—
	Porzana carolina	●	—	—	●	—
	Porphyrio martinica	●	—	—	●	—
	Gallinula chloropus	●	●	—	●	—
	Fulica americana shufeldti	—	●	—	●	—
	Aramus guarauna	—	●	—	—	—
	Grus canadensis	—	●	—	—	—
	Vanellus chilensis	●	—	—	●	—
	Charadrius vociferus	●	—	—	—	—
	Recurvirostra americana	●	—	—	—	—
	Actitis macularius	●	—	—	—	—
	Tringa solitaria	—	—	—	●	—
	Tringa melanoleuca	●	—	—	●	—
	Numenius americanus	●	—	—	—	—
	Limnodromus scolopaceus	sp.	●	—	—	—
	Gallinago delicata	●	—	—	—	—
	Scolopax minor	●	—	—	—	—
	Larus sp.	—	●	—	—	—
	Zenaida macroura	●	—	—	●	—
†	*Ectopistes migratorius*	●	●	●	—	—
	Coccyzus americanus	●	—	—	—	—
	Tyto alba	●	—	—	—	—
	Megascops asio	●	—	—	●	—
	Athene cunicularia	●	—	—	—	—
	Strix varia	—	●	—	—	—
	Asio flammeus	●	—	—	●	—
	Megaceryle alcyon	—	●	—	—	—
	Melanerpes erythrocephalus	●	—	—	—	—
	Melanerpes carolinus	—	—	—	●	—
	Picoides borealis	—	●	—	—	—
	Colaptes auratus	●	—	—	●	—
	Lanius ludovicianus	—	—	●	—	●
	Vireo griseus	●	—	—	—	—
	Cyanocitta cristata	—	—	—	●	●
	Aphelocoma coerulescens	●	—	●	—	●
	Pica hudsonia	●	—	—	—	●
	Corvus brachyrhynchos	●	—	—	●	—
	Corvus ossifragus	●	●	●	—	●
†	*Tachycineta speleodytes*	●	—	—	●	●
	Troglodytes aedon	●	—	—	—	●
	Cistothorus platensis	●	—	—	—	—
†	*Cistothorus brevis*	—	—	—	—	●
	Mimus polyglottos	●	—	—	—	—
	Toxostoma rufum	●	—	—	—	●
	Geothlypis trichas	●	—	—	—	—
	Pipilo erythrophthalmus	●	—	●	—	●
	Passerculus sandwichensis	—	—	—	●	—
	Ammodramus savannarum	●	—	—	—	—
	Ammodramus henslowii	●	—	—	●	●
	Cardinalis cardinalis	●	●	●	—	●
	Dolichonyx oryzivorus	—	—	—	—	●
	Agelaius phoeniceus	—	—	—	●	●
	Sturnella magna	●	—	—	●	●
	Quiscalus quiscula	●	—	—	—	●
	Molothrus ater	●	—	—	—	●
†	*Cremaster tytthus*	●	—	—	—	—
†	*Pandanaris floridana*	●	—	—	●	●

currently South American taxa (*Milvago chimachima, Laterallus exilis, Vanellus chilensis*), currently western prairie species (*Tympanuchus cupido, Numenius americanus, Pica hudsonia*) and boreal waterbirds that do not currently winter as far south as Florida (*Branta canadensis, Bucephala albeola, Clangula hyemalis*). The South American taxa probably indicate warmer conditions than at present, and at least *Tympanuchus cupido* would seem to indicate the presence of prairie habitat while the presence of *Pica hudsonia* might be due to the presence of megafauna. *Numenius americanus* would probably have been wintering, and its presence in Florida, east of its modern range, may be connected with the presence of extensive prairies in central North America during at least parts of the LIG (Curry & Baker, 2000; Zhu & Baker, 1995). On the whole the extralimital species suggest rather warmer conditions and the presence of more prairie habitat in central Florida than at present. The presence of boreal anatids south of their modern winter range may seem paradoxical, but is confirmed by a small LIG fauna from Chatham county in Georgia (Table 3) with *Cygnus columbianus*, well south of its modern winter range.

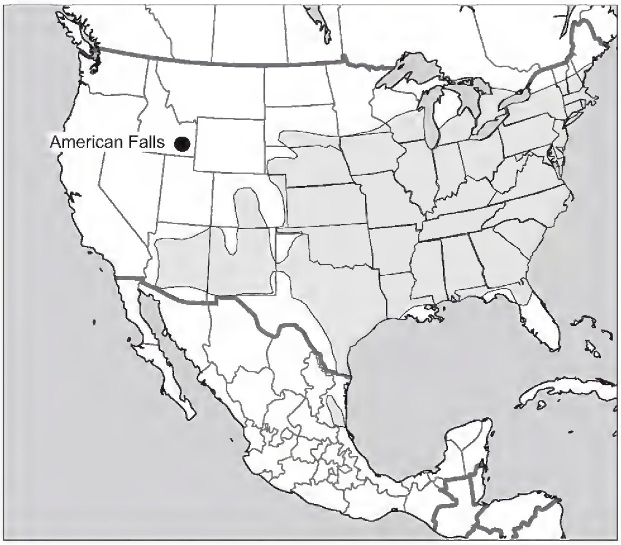

Figure 8. Modern areas of co-occurrence for the American Falls avifauna (6 analyzable taxa).

Table 3. LIG faunas from localities in Chatham County, Georgia. Source: Hulbert & Pratt (1998); ● = present.

species	Isle of Hope	Mayfair
Cygnus columbianus	—	●
Anas americana	—	●
Anas rubripes/platyrhynchos	●	—
Meleagris gallopavo	—	●

The American Falls fauna from Idaho comprises 7 taxa (one extinct) (Table 4) that define a large area of co-occurrence well to the east of the fossil site (Fig. 8). The most climatically significant taxon in the fauna is the Turkey, *Meleagris gallopavo* which has not occurred naturally in the northern Rocky Mountain area during the Holocene. Since introduced turkeys do survive in some parts of the northern Rockies the species' presence in the American Falls fauna does not necessarily indicate very different conditions from today, but the fact that the Turkey managed to disperse to Idaho presumably require the presence of at least riparian woodland corridors across the prairie zone at some stage of the Sangamonian.

The avifauna from the LIG fluvial beds of the Old Crow basin in northwestern Yukon is the only LIG arctic avifauna yet described. It is a small fauna (six species) dominated by widely distributed wetland species (Table 5).

Table 4. LIG fauna from American Falls, Idaho. Sources: Becker (1982), Brodkorb (1963), Howard (1942), Jefferson *et al.* (2002), Pinsof (1992, 1999), Steadman (1980).

American Falls, Idaho
Branta canadensis
Anas platyrhynchos
Anas sp.
Meleagris gallopavo
Ardea herodias
† *Ciconia maltha*
Cathartidae sp.

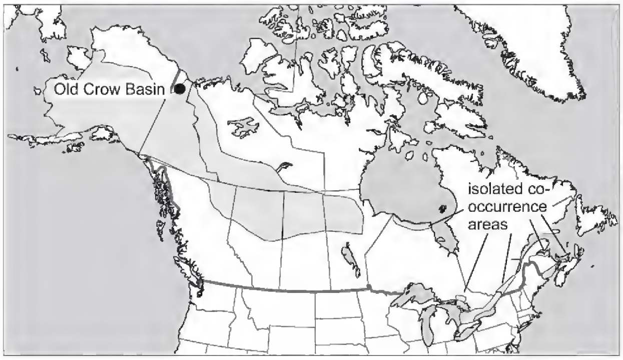

Figure 9. Modern areas of co-occurrence for the Old Crow River avifauna (6 analyzable taxa). Note the smaller isolated area south of Hudson Bay, in the St Lawrence valley and the Maritime provinces.

The LIG climate in the area was at least 2°C warmer than at present, forest reached the shore of the Arctic Ocean and large *Larix* and *Picea* logs and several southern extralimital plants and insects occur in the same layer as the birds (CAPE Last Interglacial Project Members, 2006; Harington, 1990; Matthews *et al.*, 1990). The mutual range of the avifauna (Fig. 9) is in line with this climatic information. It comprises a large part of the taiga zone but barely reaches the Old Crow River basin.

Table 5. LIG fauna from Old Crow River, Localities CRH 12,44,45,60, Yukon. Sources: Fitzgerald (1991), Harington (1989).

Old Crow River, Yukon
cf. *Anser/Chen* sp.
Anas americana
Anas clypeata
Anas [*crecca*] *carolinensis*
Anas sp.
Melanitta perspicillata
Clangula hyemalis
Tetraonidae sp.
Gavia sp.
cf. Charadriiformes sp.
Passeriformes sp.

Europe

In central Europe most of the sites with avifauna are calcareous tufas (travertines). For some reason that is not well understood, cave sites with deposits of LIG age are extremely rare if not entirely absent on the European mainland. Most or all Eemian tufa sites seem to derive from the early, warmest, part of the interglacial (pollen zones 1–4, *Helicigona banatica*-fauna (Wenzel, 2007)). This was apparently the warmest and driest part of the Eemian which in accordance with conditions in the current interglacial when tufa formation in Sweden was limited to the early part of the interglacial with a continental warm and dry climate (Gedda, 2001).

Interesting exceptions to the absence of cave faunas are two small faunas from coastal caves in Wales (Table 7). These like the Los Angeles faunas, permits comparison of landbird and seabird faunas.

Germany

The climate in Europe during the last interglacial has been well studied. During the early, warmest, part of the interglacial temperatures in central and southern Germany were about 2°C warmer than at present in summer but only slightly warmer than at present (< 1°C) in January (Aalbersberg & Litt, 1998; Kaspar *et al.*, 2005; Klotz *et al.*, 2003).

The largest German LIG avifauna is from Stuttgart-Untertürkheim (Table 6). This is a tufa fauna and the other fossils from the tufa clearly indicate a warm climate, for example Honeysuckle tree, *Lonicera arborea*, a currently Mediterranean species. The fauna contains 22 species of which 21 define an area of co-occurrence that is quite large despite the large number of species (Fig. 10), and does not indicate any definite deviation from the extant climatic conditions. The single extralimital species, *Montifringilla nivalis,* is a high-altitude montane form, which might be expected in a glacial avifauna, but not in an otherwise clearly interglacial context.

Table 6. LIG faunas from German localities. List of Localities: 1, Stuttgart-Untertürkheim, Biedermannsche Steinbruch, (Unterer Travertin); 2, Burgtonna, travertines; 3, Taubach, travertines; 4, Weimar, Parktravertin; 5. Schönfeld, Brandenburg. Sources: Adam, Bloos & Ziegler (1987); Andree (1939); Fischer (1991); Fischer & Mauersberger (1989); Heinrich (1984); Heinrich & Jánossy (1978a,b); Jánossy (1977); Lambrecht (1933); Wenzel (1998).

	Europe				
species	1	2	3	4	5
Anser anser	●	—	—	—	—
Anser sp.	●	—	—	—	—
Cygnus cygnus	—	—	cf	—	—
Cygnus sp.	●	—	—	—	—
Tadorna tadorna	—	—	cf	—	—
Anas penelope	—	—	cf	—	—
Anas platyrhynchos	●	●	●	—	—
Anas acuta	—	—	—	—	●
Aythya ferina	—	—	—	—	●?
Bucephala clangula	—	—	●	—	●
Mergus merganser	—	—	●	—	—
Perdix perdix	●?	—	—	—	—
Ixobrychus minutus	—	—	—	—	●
Pandion haliaetus	—	—	●	—	—
Accipiter nisus	—	—	—	●	—
Rallus aquaticus	●?	—	—	—	—
Porzana parva	cf	—	—	—	—
Tringa ochropus	—	—	—	—	●
Tyto alba	●?	—	—	—	—
Asio flammeus	—	—	●	—	—
Dendrocopos major	—	—	●	—	—
Eremophila alpestris	cf	—	—	—	—
Riparia/Hirundo sp.	●	—	—	—	—
Sylvia sp.	●	—	—	—	—
Erithacus rubecula	●?	—	—	—	●
Luscinia sp.	●	—	—	—	—
Oenanthe sp.	●	—	—	—	—
Turdus merula	—	—	—	—	●
Turdus iliacus	cf	—	—	—	—
Turdus philomelos	—	—	—	—	●
Sturnus vulgaris	—	—	●	—	—
Prunella modularis	—	—	—	—	●?
Prunella sp.	●	—	—	—	—
Motacilla sp.	●	—	—	—	—
Anthus pratensis	●	—	—	—	—
Anthus sp.	●	—	—	—	—
Emberiza citrinella	cf	—	—	—	—
Fringilla coelebs	●	—	—	—	—
Fringilla montifringilla	●	—	—	—	—
Loxia cf. *curvirostra*	●	—	—	—	—
Carduelis chloris	●	—	—	—	—
Pyrrhula pyrrhula	●	—	—	—	—
Coccothraustes coccothraustes	●	—	—	—	—
Fringillidae sp.	●	—	—	—	—
Montifringilla nivalis	●	—	—	—	—

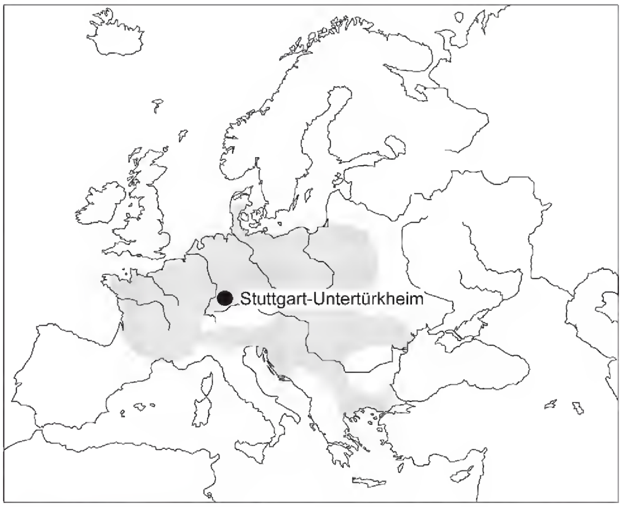

Figure 10. Modern areas of co-occurrence for the Stuttgart-Untertürkheim avifauna (22 analyzable taxa).

Table 7. LIG faunas from the coastal sites in southwest Wales: 1, Bacon Hole (Layers D–F); 2, Minchin Hole. Sources: C.J.O. Harrison (1977, 1987), Stringer *et al.* (1986), Stewart (2007).

	1	2
Calonectris diomedea	●	—
Milvus milvus	●	—
Arenaria interpres	●	—
Calidris alpina	●	●
Alca torda	●	●
Corvus corone/frugilegus	●	—
Alauda arvensis	●	●
Hirundo rustica	●	—
Oenanthe oenanthe	●	—
Turdus merula/torquatusa	●	—
Sturnus vulgaris	●	—
Sturnus cf. *unicolor*	—	●

Three tufa faunas in Thuringia (Burgtonna, Taubach, Weimar Park-Travertin) (Table 6),when merged comprise only 8 species which delineate a very large area of co-occurrence (Fig. 11). This too only confirms the generally interglacial character of the faunas, but gives no specific information about deviations in climate from modern conditions. The species reported on the basis of eggshells by Stephan (1977, 1984) were not included since the determinations were considered uncertain.

The fauna from Schönfeld in Brandenburg (nine species) (Table 6) is unusual in being derived from a lake basin.

The area of co-occurrence in this case is situated largely to the south and east of the fossil site (Fig. 12), suggesting slightly warmer and/or more continental conditions than at present.

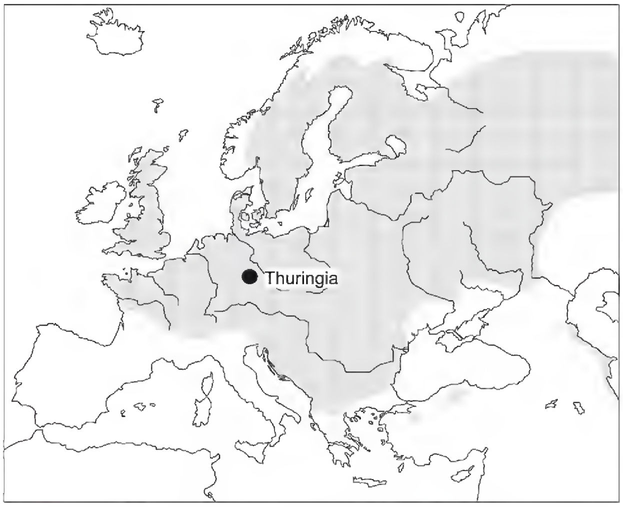

Figure 11. Modern areas of co-occurrence for the Thuringian avifaunas (Burgtonna, Taubach, Weimar) (8 analyzable taxa).

Wales

The only known European cave avifaunas of LIG age are from two coastal caves, Bacon Hole (Layer D–F) and Minchin Hole, in southwestern Wales. The combined fauna is relatively small, 10 landbird and 2 seabird taxa (Table 7), but interesting since it is the only European LIG avifauna that indicates conditions significantly warmer than at present. Both the seabirds and the landbirds suggest conditions similar to that found in parts of the Iberian peninsula today (Fig. 13).

There is a discrepancy between the LIG climate of southern England as reconstructed on the basis of palynology compared to that based on insects (Coleoptera). The latter indicate July temperatures 4°C warmer than at present (Cope, 2001) while plants indicate about 2.5°C warmer in July and 2°C colder than at present in January (Kaspar *et al.*, 2005). The birds would seem to support the higher temperatures indicated by Coleoptera. The lower temperatures suggested by the plants may be due to their lower mobility than the volant birds and insects; plants restricted to warmer habitat may simply not have had time to reach the British Isles before they were isolated by rising sea levels. This phenomenon has been noted as skewing interglacial temperature reconstructions too low in Japan (Okuda *et al.*, 2007), which is in a somewhat similar biogeographical position. Sea-surface temperatures, which are important for seabirds, were 1.5–3°C warmer than at present in summer during the LIG, while winter temperatures were similar to current conditions (Burman & Påsse, 2008).

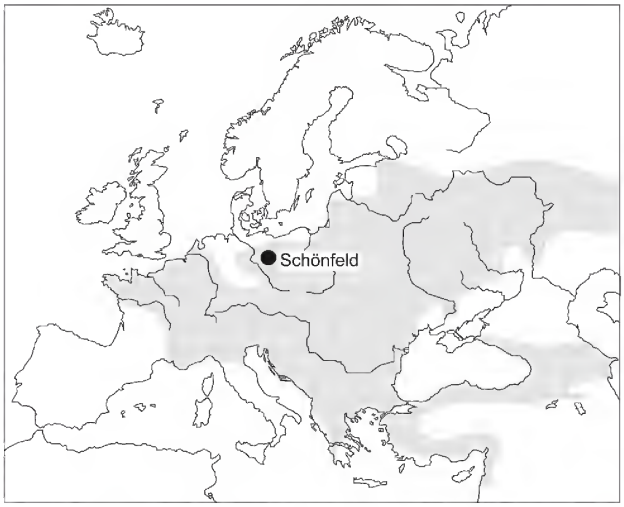

Figure 12. Modern areas of co-occurrence for the Schönfeld avifauna (9 analyzable taxa).

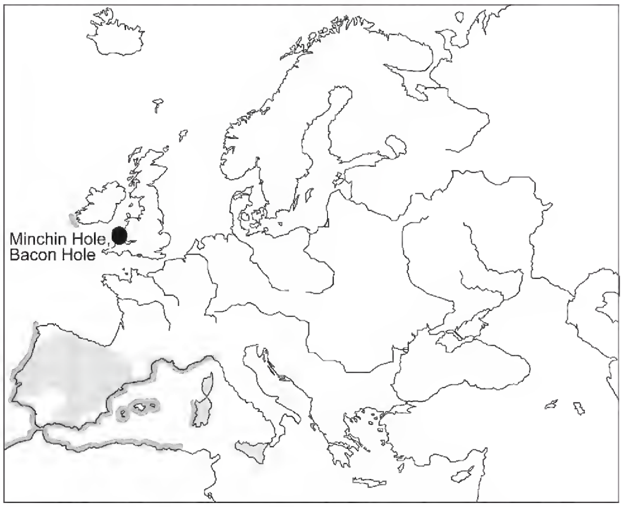

Figure 13. Modern areas of co-occurrence for the Welsh coastal cave avifaunas (Bacon Hole, Minchin Hole) (8 analyzable taxa). The shaded land area and coastal strips indicate the co-occurrence areas for landbirds and seabirds respectively.

Africa

The only African site with an appreciable LIG avifauna is Bir Tarfawi, "Grey Lake 2" deposits. At the present time Bir Tarfawi is situated in one of the most extreme desert areas on Earth, but during the LIG the area was a savannah with shallow permanent lakes. This environment indicates much higher precipitation than at present. The avifauna comprises 18 species (Table 8). 16 of which occur together today in the Sahel savannah belt where annual precipitation is in the 500–1000 mm range (Fig. 14), confirming the environmental reconstruction from other climate proxies. The two remaining species *Chlamydotis undulata* and *Pterocles senegallus,* are of special interest since they currently occur in semi-desert environment at the northern edge of the Sahara Desert (Fig. 14). The presence of these species in an otherwise Afrotropical fauna suggests that the eastern Sahara north of Bir Tarfawi was narrow during the LIG, and may not have contained any extreme desert. The fact that the fauna is predominantly Afrotropical and the few Palearctic forms are arid-adapted suggests that increased precipitation was mainly due to a northward extension of the African monsoon system rather than a southward extension of temperate weather systems from the Mediterranean. Such a northward expansion of the monsoon during the LIG has been documented from several climate proxies (Fleitmann *et al.*, 2003; Osmond & Dabous, 2004; Smith *et al.*, 2004; Szabo *et al.*, 1995) and for a brief period may even have meant a virtual disappearance of the hyperarid zone in northeastern Africa and southwestern Asia (Vaks *et al.*, 2007).

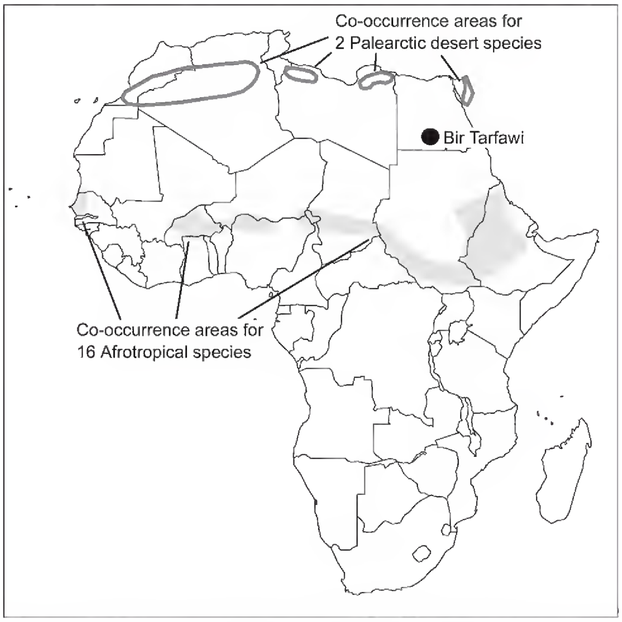

Figure 14. Modern areas of co-occurrence for the Bir Tarfawi avifauna (18 analyzable taxa). The shaded area marks the co-occurrence area for the 16 Afrotropical taxa and the unshaded area the co-occurrence area of *Chlamydotis undulata* and *Pterocles senegallus*.

Table 8. LIG fauna from Bir Tarfawi, SW Egypt. Sources: Bocheński (1991, 1993); Kowalski *et al.* (1989); G.M. Miller (1993).

Africa
Struthio camelus
Phalacrocorax africanus
Ardea cinerea
cf. *Bubulcus ibis*
Nycticorax nycticorax
Plegadis falcinellus
Gyps africanus
Turnix cf. *sylvaticusa*
Porzana cf. *pusilla*
Gallinula chloropus
Fulica cristata
Chlamydotis undulata
Pterocles cf. *senegallus*
Pterocles sp.
Oena capensis
Corvus albus
Corvus sp.
Riparia cf. *riparia*

New Zealand

The only avifauna from the southern hemisphere that is reasonably securely dated to the LIG and large enough for environmental reconstruction is from Cape Wanbrow on New Zealand.

The LIG climate of New Zealand was 2–3°C warmer than at present (Marra, 2003) while sea-surface temperatures were about 1°C warmer than at present in the Tasman Sea immediately west of New Zealand (Pelejero *et al.*, 2006).

The fauna comprises 11 species, five landbirds and six seabirds (Table 9), of which four and one respectively have gone extinct during the late Holocene. Because the modern range of extinct species cannot be defined, only the common foraging range of the seabird component of the fauna can be determined (Fig. 15). This comprises the coastal waters around most of New Zealand, and does not indicate any significant difference compared to modern conditions.

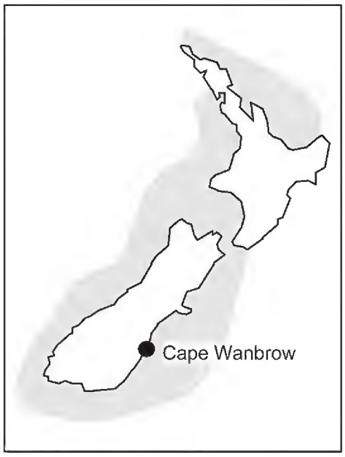

Figure 15. Modern area of co-occurrence for the Cape Wanbrow marine avifauna (5 analyzable taxa).

Table 9. LIG fauna from Cape Wanbrow (sites J41/f8710, f8214, f8227), New Zealand. Sources: Worthy & Grant-Mackie (1993); Boessenkool *et al.* (2008).

New Zealand
† *Emeus crassus*
† *Pachyornis elephantopus*
† *Megadyptes waitaha*
Eudyptula minor
Puffinus griseus
Puffinus gavia/huttoni
Pelecanoides urinatrix
Phalacrocorax punctatus
† *Harpagornis moorei*
Nestor meridionalis
† *Sceloglaux albifacies*

Discussion

Initially it must be noted that the identification of the studied sites as being of LIG age on biostratigraphic and chronostratigraphic grounds is confirmed by the avifaunas. Only in two cases are there records of species that seem out of place in a fully interglacial environment, Arredondo IA (*Bonasa umbellus*) and Stuttgart-Untertürkheim (*Montifringilla nivalis*).

The avifaunas also mostly conform quite well to the environmental and climatic conditions indicated by other proxies. However, in some cases the avifaunas suggest differences between modern and LIG conditions that are not obvious in earlier reconstructions, for example the presence of wetlands in the Los Angeles area, prairie habitat in northern Florida and the presence of desert taxa with northern affinities in the Bir Tarfawi area.

One somewhat mysterious matter is the presence of boreal swans, geese and ducks south of their present winter range in eastern North America. A possible explanation might be that the known very warm arctic LIG climate (e.g., CAPE Last Interglacial Project Members, 2006) meant much larger breeding populations, which needed larger wintering areas than the extant populations. Another possible explanation is increased seasonality. There is some evidence for this from southern Europe where winter temperatures seems to have been lower than at present at the beginning and the end of the LIG when winter insolation was low at mid-latitudes, despite summer and annual average temperatures being higher than at present (Allen & Huntley, 2009; Rousseau *et al.*, 2006).

As for the effect of the generally warmer climate during the LIG it seems clear that differences on the order of 2°C or less, both on land and in sea-surface temperatures, are barely, if at all, detectable in the avifaunas. The Old Crow River fauna, with a temperature differential probably slightly more than 2°C seems to be a borderline case.

It is unfortunate that there are no quantitative data on LIG climate in Florida, since the faunas there show small but significant differences compared to modern faunas from the same area.

On the other hand the Welsh coastal faunas show a quite clear climatic signal, which is associated with a summer temperature differential of 4°C, judged by the entomological data.

The strongest climatic signal by far is of course the one connected to the Bir Tarfawi fauna which is completely different from the (almost nonexistent) fauna occurring in the area today. In this case it is however, not the temperatures but the precipitation that is the determining factor.

It might be noted in this context that a recent very thorough review of changes in numbers and distribution of the Swedish avifauna during the last 30 years failed to find any identifiable effects of climatic change, though the average annual temperature has risen nearly 1°C during this period (Ottvall *et al.*, 2009).

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Cracking a Developmental Constraint: Egg Size and Bird Evolution

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ABSTRACT. It has been suggested that relative egg size in living birds is strongly correlated with the developmental mode of the young; "altricial" (helpless) or "precocial" (independent). Using a data set of extant taxa we show that altricial birds lay relatively larger eggs than their precocial counterparts but that this may be due to the small size of most altricial species. Smaller birds tend to lay relatively small eggs compared to large species. Nonetheless, a predictive egg mass-body mass relationship extends into the avian fossil record. Such a relationship is important to our understanding of avian evolution because relative egg size (and thus available developmental mode) was constrained in many early birds—oviduct diameter was limited by the presence of pubic fusion. Therefore we document the evolution of avian developmental strategies using morphology-based phylogenies for Mesozoic and extant avians and corroborate correlations between developmental strategies, egg weight and female body mass. The sequential loss of precocial features in hatchlings characterises the evolution of birds while altriciality is derived within Neoaves. A set of precocial strategies is seen in earlier lineages, including basal Neornithes (modern birds) and are implied in their Mesozoic counterparts—skeletal constraints on egg size, present in many Jurassic and Early Cretaceous birds (*Archaeopteryx, Confuciusornis*, Enantiornithes) were lost in later diverging lineages. Attributes of precociality were already present in a number of lineages of non-avian maniraptoran theropods. We propose that the evolution of "unrestricted egg size" may have precipitated subsequent development of the diverse reproductive strategies seen in living birds.

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Birds are unique amongst living vertebrates in the sheer range of developmental strategies and forms of parental care they employ (O'Connor, 1994). This variation, spread across a spectrum that ranges from completely helpless hatchlings ("altricial") to those that are independent, even immediately flighted ("precocial"), has always proved difficult to classify and understand in a phylogenetic context even when dealing with modern birds (living Neornithes) (Nice, 1962; O'Connor, 1994; Starck & Ricklefs, 1998). This is because avian developmental strategies are not always consistent within families and are a mixture of behavioural and physiological phenomena (Starck & Ricklefs, 1998). Consequently there has been little evidence of any directional trend when characteristics of this altricial-precocial (A–P) spectrum (effectively degree of "neonate dependence") have been mapped onto the various phylogenies proposed for birds (Aves) during the 20th century (Cracraft, 1986; Starck & Ricklefs, 1998; Sibley & Ahlquist, 1990; Deeming, 2007a).

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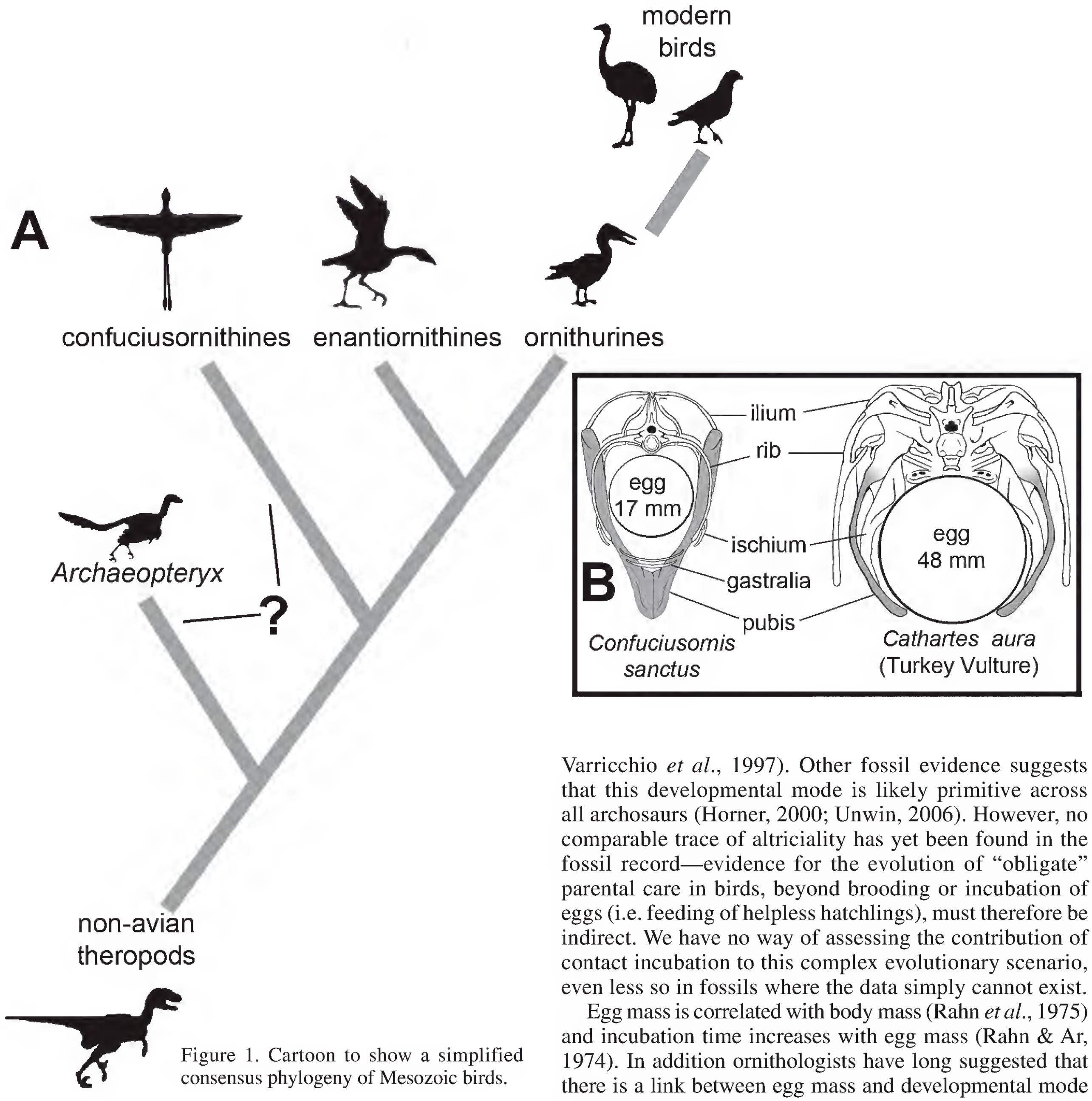

Figure 1. Cartoon to show a simplified consensus phylogeny of Mesozoic birds.

We also note that the actual characteristics that determine "altriciality" and "precociality" are not absolute: even simple characteristics are subject to observational judgment and are not exactly the same in one lineage of birds as they are in another (Starck & Ricklefs, 1998).

Nevertheless, in spite of a lack of clear phylogenetic association, it has long been suggested that "precociality" is the primitive condition within Aves (Elzanowski, 1981; Starck & Ricklefs, 1998; Zhou & Zhang, 2004). Well-developed feathers in a late-stage embryo of a Cretaceous enantiornithine even suggest "super-precociality" (immediate flight) at hatching in at least one pre-neornithine fossil bird (Zhou & Zhang, 2004). Taken in combination with inferred osteological growth rates for other fossil birds (Chinsamy, 2002; de Ricqlès *et al*., 2003; Cambra-Moo *et al*., 2006), and the egg and nest morphologies of some non-avian theropods, evidence clearly points to precociality at the base of Aves (Elzanowski, 1981; Varricchio *et al*., 1997). Other fossil evidence suggests that this developmental mode is likely primitive across all archosaurs (Horner, 2000; Unwin, 2006). However, no comparable trace of altriciality has yet been found in the fossil record—evidence for the evolution of "obligate" parental care in birds, beyond brooding or incubation of eggs (i.e. feeding of helpless hatchlings), must therefore be indirect. We have no way of assessing the contribution of contact incubation to this complex evolutionary scenario, even less so in fossils where the data simply cannot exist.

Egg mass is correlated with body mass (Rahn *et al*., 1975) and incubation time increases with egg mass (Rahn & Ar, 1974). In addition ornithologists have long suggested that there is a link between egg mass and developmental mode (Heinroth, 1922; Amadon, 1943; Tullberg *et al*., 2002). Although Rahn & Ar (1974) were unable to detect such a relationship, it is supported by other evidence (Nice, 1962; Starck & Ricklefs, 1998; Deeming, 2007ab). If significant, a predictive relationship would be hugely important to interpreting the avian fossil record because of anatomical constraints on egg size (Fig. 1B), exceptional flightless living birds like the kiwi, *Apteryx*, notwithstanding. Here we restrict our discussion to flighted birds where egg size is also constrained by aerodynamic considerations.

In this paper we reconstruct the evolution of the A–P spectrum in living neornithine birds by mapping the distribution of neonate dependence (Nice, 1962; O'Connor, 1994; Starck & Ricklefs, 1998; Deeming, 2007a) onto a recent morphology-based phylogeny (Livezey & Zusi, 2006, 2007) (Fig. 2). Trends were cross-checked against another recent large-scale genomic study that reconstructed the phylogenetic history of birds (Hackett *et al*., 2008). We then corroborate the presence of previously suggested correlations

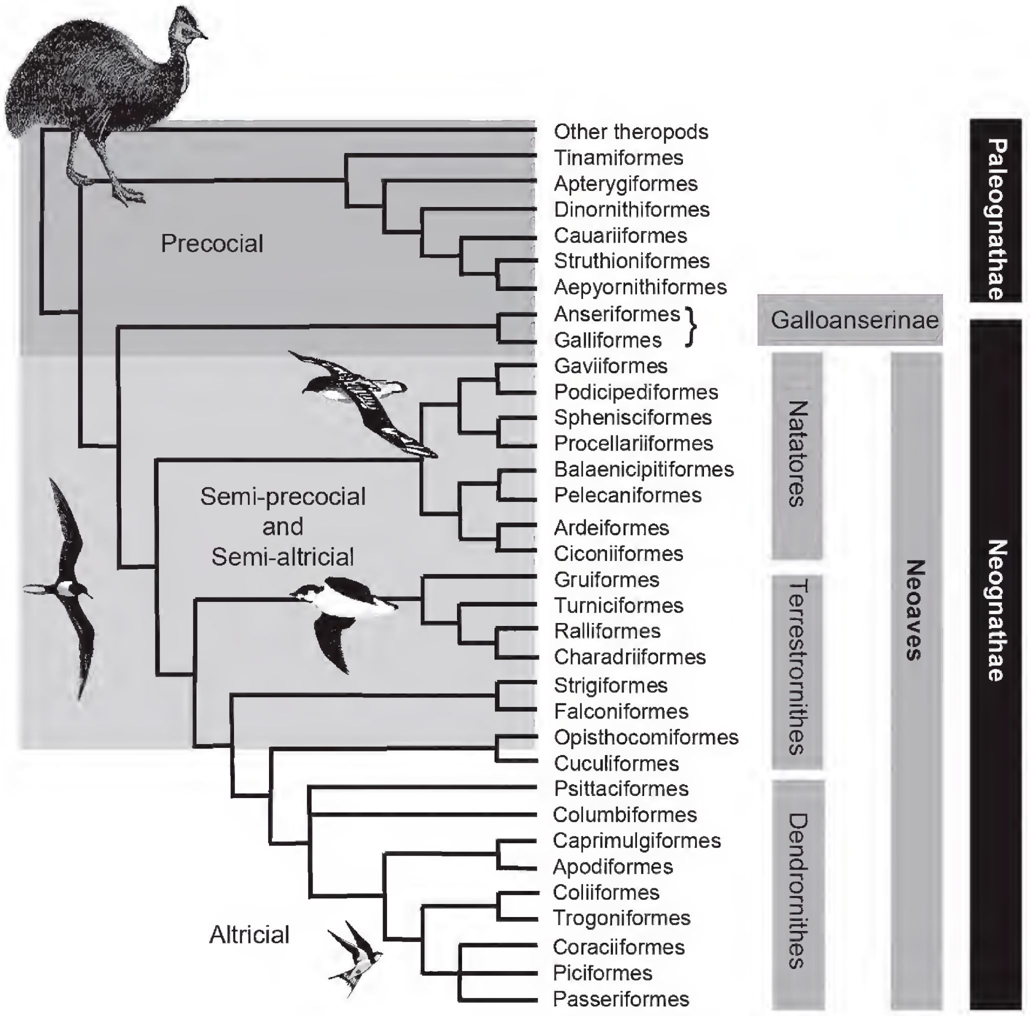

Figure 2. Phylogenetic hypothesis for relationships amongst modern birds (Neornithes) showing altricial and precocial modes of development (Livezey & Zusi, 2006, 2007).

between egg mass and female body mass (Appendix) as proxies for avian parental investment (Deeming, 2007ab). Finally, using femur length to approximate body mass (Hone *et al*., 2008), we added data for specimens of the abundant and early diverging Cretaceous bird *Confuciusornis* (Appendix) to extend this predictive relationship back into the avian fossil record and to augment our understanding of the theropod origin of birds.

Materials and methods

Our analyses use egg mass and female body mass data for species-level taxa culled from the primary literature and from Dunning (1993; see also Appendix), correlated with the morphology-based phylogeny of Livezey & Zusi (2006, 2007). Data coverage across the major neoavian clades is good, but for this analysis we only have a small (N=2) sample for paleognaths. For the well-represented fossil bird *Confuciusornis*, egg volume was calculated from the measured width of the pelvic canal and extrapolated proportions of modern bird eggs and egg mass from a standard shape/volume equation (Hoyt, 1979). We know (Kaiser, 2007) that the eggs of these Cretaceous birds were more-or-less round, as are those of described enantiornithines (Zhou & Zhang, 2004). Avian femur lengths were extracted from a published compilation (Dyke *et al*., 2006) and the RBCM ornithology collection while fossil body mass estimates were calculated using a standard allometric method (Hone *et al*., 2008). *Confuciusornis* specimen measurements are from Kaiser (2007) and Hone *et al*. (2008), cross-checked with Chiappe *et al*. (1999). Because this paper discusses initial qualitative comparisons, at a very broad phylogenetic scale, a comparative analysis is not presented. This represents an area for future work.

Results and discussion

Extant birds (living Neornithes)

In contrast to earlier studies of avian developmental evolution that require multiple origins of altriciality in birds (Starck & Ricklefs, 1998; Deeming, 2007ab), simple qualitative mapping of neonate dependence onto the phylogenetic hypothesis of Livezey & Zusi (2007) is appropriate because this topology implies a sequential loss of precocial features towards the crown of Neoaves (Fig. 2). Earlier diverging lineages of Neornithes (Paleognathae, Galloanserinae, Gaviiformes, and Podicipediformes) are characterized by a high degree of precociality (del Hoyo *et al*., 1992–2002; Starck & Ricklefs, 1998). The young of the Pelecaniformes, a later diverging member of the Natatores (Livezey & Zusi, 2007), are the first to exhibit altriciality. The degree of altriciality is highly variable among the Natatores, and often restricted to the early neonate stages, as in the Sphenisciformes (penguins) and Procellariiformes (petrels). Later stages are typically active and mobile (Dunn, 1975; Simpson, 1976; Warham, 1990; Gaston, 2004). Later diverging groups, such as those clustered in the Terrestrornithes also exhibit varying degrees of altriciality. In contrast, it does appear to be the case that completely helpless hatchlings—born naked, blind and immobile—characterize the large monophyletic cluster of small, forest-dwelling birds at the crown of Neoaves, Dendrornithes (Fig. 2), although more data combined with a phylogenetic comparative analysis will be require to verify this correlation. The most significant incompatibility between our qualitative mapping of neonate dependence (qualitative data from Kaiser, 2007) onto the morphology-based phylogeny of Livezey & Zusi (2007) or the phylogenomic result of Hackett *et al.* (2008), relates to the crownward movement of falconids, which places a group with "semi-altricial" developmental strategies (sensu Starck & Ricklefs, 1998) as the closest relative to two other clades (Passeriformes and Psittaciformes) that have fully altricial young. This correlation is intuitive.

The evolutionary transition from precociality to altriciality, correlated with changes in relative egg-size, is not the only aspect of avian reproduction that can be accommodated by phylogeny (Livezey & Zusi, 2006, 2007); broad qualitative trends in duration of incubation and enhanced nestling-care, increasingly sophisticated nest-building and decreases in clutch size are also apparent (Fig. 2). Some of these may be related to an overall decrease in adult size associated with a shift from relatively simple, open environments to the complex three-dimensional structure of tree canopies. As expected from their less-developed hatchlings, the eggs of altricial birds require shorter incubation periods (on average 20.8 days, n = 18 non-passerine birds). All Passeriformes produce altricial young and some have extremely short incubation periods, between 10 and 16 days (Skutch, 1945) although this may reflect their small body and eggs (Kaiser, 2007). Birds that produce precocial young incubate their eggs for somewhat longer periods (23.2 days, n = 5). Semi-precocial and semi-altricial young appear to be incubated for even longer periods; 24.4 days (n = 23) and 32.3 days (n = 42) days respectively (del Hoyo *et al.*, 1992–2002). Interestingly, Grellet-Tinner *et al.* (2006) documented a clear egg-size increase within oviratorid non-avian theropods that they suggested could have occurred to accommodate additional nutrients within the egg

Small adult body size and intense parental care in altricial taxa may combine to produce shorter periods of nestling dependence (28.5 days) than in semi-precocial (40.3 days) or semi-altricial birds (42.2 days) although this is likely phylogenetically constrained (Deeming *et al.*, 2006). At a very broad level, early diverging precocial birds, and later diverging semi-precocious and semi-altricial taxa, use unsophisticated nests that simply keep their eggs from rolling away. These "nests" tend to be limited to scrapes, cushions of feathers and plant stems, or simple platforms of twigs placed out in the open. At best, they are camouflaged or hidden by adjacent vegetation. A wide range of birds hides its nests in tree cavities, underground burrows, or rock crevices. Some tree cavities boast a thick mattress of feathers but most are bare and many burrow nesters, especially seabirds, place their eggs on the ground, with only a thin pad of vegetation for protection (Warham, 1990; Gaston, 2004). It is only among the most crownward and wholly altricial taxa that we find elaborately constructed woven and moulded nests, an elaboration of the trend noted in non-avian theropod dinosaurs by Grellet-Tinner *et al.* (2006). Indeed, this trend, in particular, may prove related again to body size: more complex nests may represent a response to the thermal issues related to small parental size. This represents another area for future work.

Interpreting the avian fossil record

Of clear significance for interpreting the fossil record, our data demonstrate that within the neoavian clade, "fully altricial" birds (*sensu* Nice, 1962; Starck & Ricklefs, 1998; Deeming, 2007a) produce significantly larger eggs (compared to female body mass) (Fig. 3A,B), than those of "precocial" and "super precocial" taxa. However such results likely reflect two distinct evolutionary trends. The first reflects the preponderance of precocial neonates among basal clades and altricial neonates among crown clades. The second reflects trends in body size and a bias in the distribution of body masses among living birds. Members of basal clades tend to be larger than members of crown clades. Both with in clades and across class Aves, larger birds have lower egg to body ratios. A sub-sample of birds of comparable weights shows little difference in relative egg size between groups with altricial and precocial strategies. It is more supporting of the conclusions of Faaborg (1988) or Tulberg *et al.* (2002) that larger eggs are necessary for the pre-hatching development of precocial young.

Perhaps of greater evolutionary significance is the tendency of birds (within the subset of birds of comparable weight) that use either semi-altricial or semi-precocial strategies to have relatively large eggs. Some of these groups [e.g., Procellariiformes, Alcidae (Charadriiformes), Phaethontidae (Pelecaniformes)] combine relatively large eggs with minimal clutch sizes (1 or 2).

Combined with the concentration of altricial strategies in smaller birds, our data suggest the possibility of a lower limit on absolute egg size that may preclude precociality in most birds. Final adult body size is also much closer to the mass of the hatchling in small altricial birds than it is in their precocial counterparts (Deeming & Birchard, 2007), suggesting that time-to-independence is also a limiting factor on avian relative egg mass.

Using femur length as a proxy for body mass the predictive relationship between egg mass, body mass and reproductive strategy (Fig. 3) can be extended into the fossil record (Fig. 4). Although this proxy approach does not allow the subdivisions of the A–P spectrum to be distinguished (Appendix), it can be used to extrapolate egg mass relative to body mass across Aves. Corroborated by its pelvic anatomy (Fig. 1B), the relative egg size of the basal Early Cretaceous fossil bird *Confuciusornis*, for example, was small in comparison to that of most living birds (Fig. 4). Constrained by their anatomy, relatively small eggs must characterize most of the early diverging avian lineages (Fig. 1). In *Confuciusornis*'s case, in combination with its inferred growth rate (de Ricqlès *et al.*, 2003; Cambra-Moo *et al.*, 2006) and phylogenetic position (Chiappe *et al.*, 1999; Zhou & Zhang, 2004; Gao *et al.*, 2008) this bird was almost certainly precocial (Fig. 1). Recent studies also determined the growth rate of *Confuciusornis* to have been slower than that of many extant birds (Cambra-Moo *et al.*, 2006): this would also be reflected in extended time-to-independence for its nestlings as is seen in modern precocial birds. *Confuciusornis* appears to have laid an egg comparable in size to that of the extant Buttonquail (genus *Turnix*) even though the adult Buttonquail is a much smaller animal.

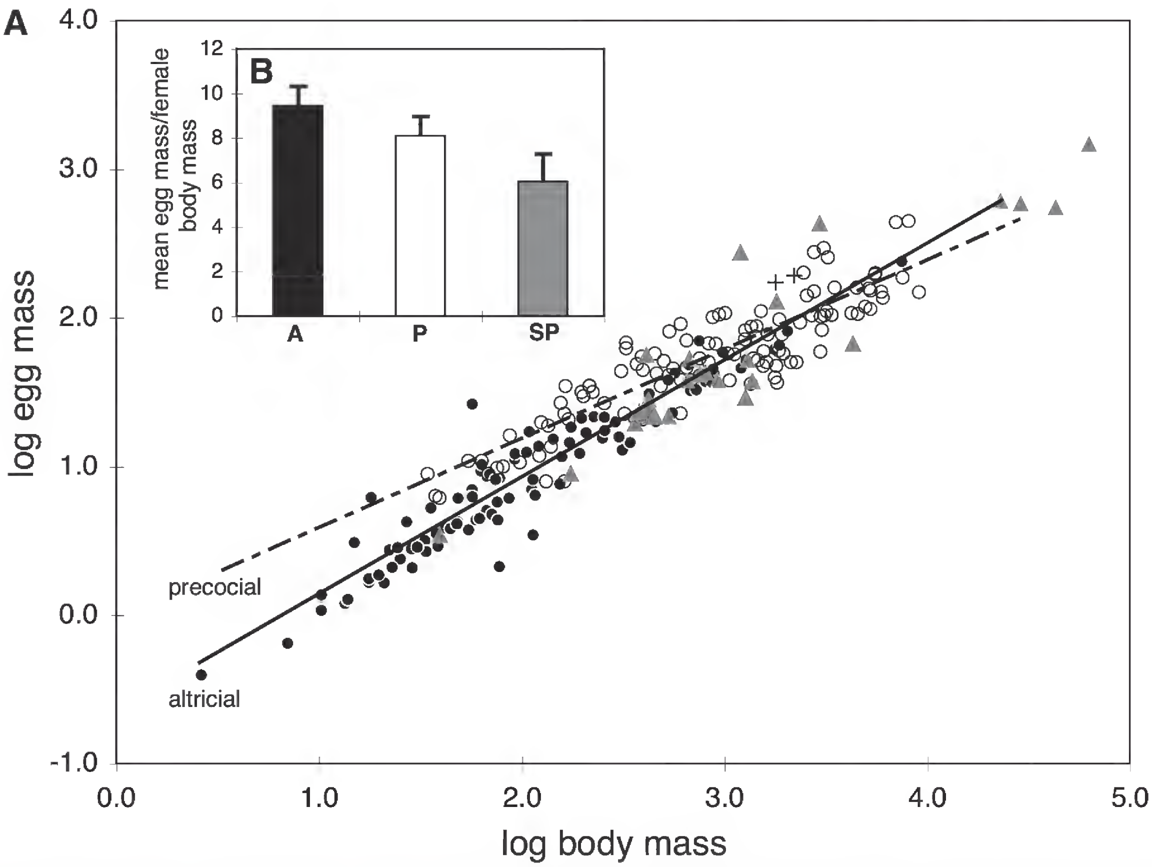

Figure 3. Relationship between egg weight and female body weight in extant birds. (A) Graph to discriminate between altricial [n = 96; filled circles; $r^2 = 0.906$, $p < 0.001$; egg mass = –0.659394 + 0.7889097.bodymass], and precocial [n = 113; open circles] (including super precocial [n = 29; grey triangles]; $r^2 = 0.801$, $p < 0.001$; egg mass = –0.164615 + 0.6451872.bodymass) taxa. Both of these results have significantly higher r^2 values than those found for 100 bootstrap replicates that paired body and egg mass at random. (B) Bar chart showing that the three broad developmental modes seen in Neornithes are characterized by significantly different egg/female body mass relationships. Discrimination among all three groups is borne out by averaged data (Kruskal-Wallis test, $p < 0.005$). Abbreviations: A, altricial; P, Precocial; SP, super precocial.

However, the hatchlings of *Confuciusornis* appear to have taken about five times as long to reach their adult size based on an estimate for *Confusiusornis* of 20 weeks (Cambra-Moo *et al.*, 2006) compared to three weeks from hatching to full independence in *Turnix* (Debus, 1996).

Origin of avian neonate adaptations and survivorship

Even in the absence of direct fossil evidence, small relative egg size in basal birds (including *Confuciusornis*) is expected: the eggs of comparably-sized dinosaurs close to the theropod-bird transition were also small (Buffetaut *et al.*, 2005). Indeed, phylogenetic studies predict that in addition to the acquisition and refinement of feathers, retention of a basal small body size was paramount at the "theropod-bird evolutionary transition" (Turner *et al.*, 2007) (Fig. 1). Of course the evolution of feathers would also allow for better heat retention at relatively smaller body sizes while the neonates of many non-avian theropod dinosaurs are known to have been extremely "birdlike"—evidence for precociality in baby theropod dinosaurs comes from osteology and even posture (Xu & Norell, 2004). In addition, just like modern birds, maniraptoran theropods are known to have laid eggs from a single functional oviduct (Varricchio *et al.*, 1997, Grellet-Tinner & Makovicky, 2006; Grellet-Tinner *et al.*, 2006) and in some cases are thought to have cared for their young (Horner, 2000). As far as is known simple nesting structures also characterize both non-avian theropods and basal birds (Grellet-Tinner *et al.*, 2006); there are no known Mesozoic examples of elaborately constructed nest structures comparable to the woven nests of modern Passerformes (Fig. 3).

Mirroring our "egg size-neonate dependence" hypothesis at the reproductive level, the production of diminutive eggs by early birds is anatomically consistent with the pubic fusion (symphysis) seen in early diverging Jurassic and Cretaceous taxa (i.e. *Archaeopteryx, Confuciusornis*, known enantiornithines) and recorded as characters in phylogenetic hypotheses (e.g., Gao *et al.*, 2008): the presence of this rigid pubic structure would have limited the maximum diameter of the egg passing through the oviduct. Some non-avian dinosaurs appear to have attempted to overcome the effects of this constraint by producing elongated eggs that could contain more nutrient than a spherical egg of the same diameter (Grellet-Tinner *et al.*, 2006). Modern avian embryos develop their lightweight skeletons from calcium extracted from the eggshell. The increased surface to volume ratio of elongated dinosaur eggs might have made more calcium available to an embryo developing a long bony tail and the relatively heavy skeleton of a terrestrial animal. Because there is a relationship between egg size and neonate dependence, loss of this structural constraint in the Mid- to Late Cretaceous enabled the production of larger eggs and must have contributed to—even precipitated—the

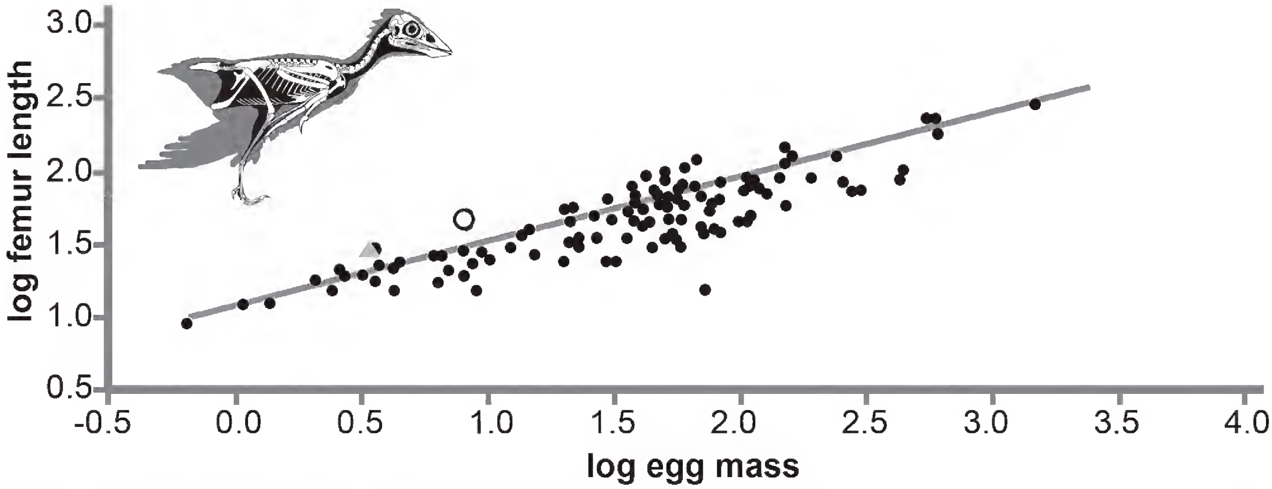

Figure 4. Relationship between femur length (approximates body mass) and egg mass in extant and fossil birds ($n = 117$; $r^2 = 0.758$, $p < 0.001$). These data show that both *Confuciusornis* (cartoon, open circle) and the similarly-sized Buttonquail (*Turnix*) (grey triangle) lay relatively small eggs compared to their body size (Appendix).

subsequent proliferation of avian reproductive strategies. Reduction of constraints on egg size and thus neonate dependence in ornithurine and basal neornithine birds also provides a possible explanation for the "selective survivorship" of modern birds in the aftermath of the end-Cretaceous extinction event.

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Appendix

Data used in the paper. Confuciusornis egg measurement from Kaiser (2007; Kenya Museum number B072). Femur lengths (N=15) from Hone *et al.* (2008), with mean length value verified by Chiappe *et al.* (1999). Abbreviations for development categories are *a*, altricial; *p*, precocial; *sa*, semi-altricial; *sp*, semi-precocial. The last column shows mean femur length and sample size.

species	development category	egg mass (g)	female mass (g)	log female mass	log egg mass	egg / female mass %	mm (n) mean femur
Accipiter badius	a	21.3	196	2.2923	1.3291	10.9	
Accipiter brevipes	a	21.7	254	2.4048	1.3357	8.5	
Accipiter cooperii	a	43.0	566	2.7528	1.6335	7.6	64.9 (15)
Accipiter gentilis	a	59.0	973	2.9880	1.7709	6.1	82.8 (11)
Accipiter striatus	a	18.5	174	2.2405	1.2672	10.6	48.4 (24)
Alcedo atthis	a	4.3	27	1.4314	0.6340	15.9	15.3 (3)
Alectoris barbara	p	21.9	376	2.5752	1.3407	5.8	
Alectoris chukar	p	22.0	453	2.6556	1.3424	4.9	61.0 (1)
Alectoris graeca	p	21.8	530	2.7243	1.3376	4.1	56.8 (1)
Alectoris rufa	p	21.6	453	2.6556	1.3341	4.8	55.4 (1)
Alectura lathami	sp	192.0	2210	3.3444	2.2833	8.7	89.5 (1)
Anas acuta	p	41.6	755	2.8779	1.6191	5.5	46.6 (2)
Anas americana	p	52.9	672	2.8274	1.7237	7.9	43.0 (8)
Anas clypeata	p	37.8	653	2.8149	1.5775	5.8	41.4 (5)
Anas discors	p	28.1	422	2.6253	1.4487	6.7	32.9 (3)
Anas platyrhynchos	p	52.2	1301	3.1143	1.7177	4.0	48.1 (7)

species	development category	egg mass (g)	female mass (g)	log female mass	log egg mass	egg / female mass %	mm (n) mean femur
Anas strepera	p	43.1	808	2.9074	1.6345	5.3	44.1 (4)
Anhinga anhinga	sa	36.3	1338	3.1263	1.5599	2.7	53.8 (6)
Anser albifrons	p	128.5	1809	3.2574	2.1089	7.1	70.9 (1)
Aphelocoma californica	a	6.2	86	1.9337	0.7924	7.2	
Aphelocoma coerulescens	a	5.8	75	1.8749	0.7642	7.7	
Aphelocoma insularis	a	7.1	111	2.0461	0.8507	6.4	
Aphelocoma ultramarina	a	8.2	113	2.0519	0.9149	7.3	
Apteryx australis	p	430.0	2955	3.4706	2.6335	14.6	90.3 (5)
Apteryx owenii	p	275.5	1200	3.0792	2.4401	23.0	76.3 (2)
Apus affinis	a	2.4	25	1.3979	0.3825	9.7	15.4 (1)
Apus apus	a	3.6	38	1.5752	0.5539	9.5	17.5 (3)
Apus caffer	a	2.8	22	1.3444	0.4436	12.6	
Apus melba	a	6.2	18	1.2529	0.7955	34.9	
Apus pallidus	a	3.9	42	1.6222	0.5904	9.3	
Aramus guarana	sa	57.4	1110	3.0453	1.7589	5.2	76.5 (2)
Ardea alba	sa	39.4	812	2.9096	1.5956	4.9	
Ardea cinerea	sa	60.3	1547	3.1893	1.7800	3.9	102.8 (3)
Ardea herodias	sa	50.7	2110	3.3243	1.7053	2.4	99.4 (16)
Ardea purpurea	sa	50.8	830	2.9191	1.7055	6.1	87.3 (3)
Ardeotis arabs	p	107.5	4500	3.6532	2.0314	2.4	
Ardeotis kori	p	151.1	5900	3.7709	2.1793	2.6	145.0 (1)
Balaeniceps rex	sa	159.5	5130	3.7101	2.2028	3.1	127.0 (1)
Bombycilla cedrorum	a	3.2	33	1.5198	0.5051	9.7	19.1 (2)
Bombycilla garrulus	a	3.8	54	1.7340	0.5798	7.0	22.3 (1)
Botaurus lentiginosus	sa	35.1	482	2.6830	1.5452	7.3	
Botaurus stellaris	sa	42.0	867	2.9380	1.6232	4.8	94.6 (4)
Burhinus oedicnemus	p	42.8	459	2.6618	1.6310	9.3	
Cacatua sanguinea	a	23.1	550	2.7404	1.3644	4.2	
Cacatua tenuirostris	a	20.3	455	2.6580	1.3064	4.5	
Calyptorhynchus banksii	a	33.2	720	2.8573	1.5209	4.6	
Calyptorhynchus latirostris	a	32.8	675	2.8293	1.5163	4.9	
Caprimulgus aegyptius	a	8.4	77	1.8882	0.9267	10.9	
Caprimulgus carolinensis	a	17.3	108	2.0330	1.2376	16.0	
Caprimulgus europaeus	a	8.7	67	1.8261	0.9397	13.0	23.4 (2)
Caprimulgus ridgwayi	a	4.3	48	1.6812	0.6311	8.9	21.5 (1)
Caprimulgus ruficollis	a	9.2	69	1.8357	0.9651	13.5	
Caprimulgus vociferus	a	7.0	57	1.7520	0.8481	12.5	21.0 (2)
Casuarius casuarius	p	584.0	29000	4.4624	2.7664	2.0	232.0 (1)
Cathartes aura	a	82.1	2033	3.3081	1.9143	4.0	71.7 (12)
Centropus senegalensis	a	11.7	156	2.1931	1.0700	7.5	
Chlamydotis undulata	p	52.4	1450	3.1614	1.7192	3.6	65.5 (2)
Chlidonias hybrida	p	16.3	87	1.9370	1.2122	8.1	
Chlidonias leucoptera	p	11.0	54	1.7324	1.0414	20.4	
Chlidonias niger	p	11.0	63	1.7987	1.0414	17.5	
Chlorostilbon mellisugus	a	0.4	3	0.4150	-0.3979	15.4	
Ciconia ciconia	sa	105.9	3350	3.5250	2.0248	3.2	94.0 (1)
Ciconia nigra	sa	83.9	3000	3.4771	1.9236	2.8	85.0 (3)
Coccyzus americanus	*a*	*9.4*	*63*	*1.7966*	*0.9731*	*15.0*	*27.9 (2)*
Coccyzus erythropalmus	a	6.3	56	1.7443	0.7993	11.4	26.4 (1)
Coccyzus minor	a	9.0	69	1.8388	0.9518	13.0	
Columba livia	a	14.6	340	2.5315	1.1644	4.3	39.0 (4)
Coracias benghalensis	a	14.6	171	2.2330	1.1643	8.5	
Coracias garrulus	a	15.4	142	2.1523	1.1872	10.8	26.8 (1)
Cuculus canorus	a	3.5	113	2.0531	0.5434	3.1	28.9 (2)
Cuculus saturatus	a	2.1	77	1.8865	0.3313	2.8	
Cursorius cursor	sa	13.7	138	2.1399	1.1379	10.0	
Cypseloides niger	a	5.3	35	1.5490	0.7243	15.0	
Dendragapus obscurus montana	p	28.8	1271	3.1041	1.4594	2.3	68.2 (1)
Diomedea chlororhynchos	sp	202.9	2434	3.3863	2.3073	8.3	
Diomedea epomophora	sp	452.5	8040	3.9053	2.6556	5.6	
Diomedea exulans	sp	445.0	6950	3.8420	2.6484	6.4	103.0 (4)
Diomedea immutabilis	sp	279.0	2750	3.4393	2.4456	10.1	72.7 (19)
Diomedea melanophris	sp	258.0	3206	3.5060	2.4116	8.0	84.0 (1)
Diomedea nigripes	sp	298.0	3069	3.4870	2.4742	9.7	77.6 (18)
Dromaeus novaehollandiae	p	550.0	43080	4.6343	2.7404	1.3	227.9 (11)
Eolophus roseicapillus	a	13.0	311	2.4928	1.1153	4.2	
Falco mexicanus	a	37.6	801	2.9036	1.5752	4.7	73.3 (9)
Falco peregrinus	a	46.4	1201	3.0795	1.6665	3.9	73.0 (10)
Falco rusticolis	a	62.0	1748	3.2425	1.7923	3.5	88.1 (9)
Falco sparverius	a	13.8	120	2.0792	1.1399	11.5	36.6 (15)
Francolinus africanus	p	19.5	362	2.5581	1.2897	5.4	
Francolinus bicalcaratus	p	23.3	381	2.5809	1.3682	6.1	
Francolinus francolinus	p	24.3	424	2.6274	1.3861	5.7	
Fregata magnificens	a	88.2	1344	3.1282	1.9453	6.6	
Fregata minor	a	88.8	1428	3.1546	1.9484	6.2	49.7 (1)

species	development category	egg mass (g)	female mass (g)	log female mass	log egg mass	egg / female mass %	mm (n) mean femur
Gavia adamsii	p	153.5	5212.5	2.18611	3.71705	2.9	64.1 (1)
Gavia immer	p	152.5	2740	2.18327	3.43775	5.6	58.5 (1)
Gavia pacifica (arctica)	p	98.4	1850	1.993	3.26717	5.3	41.8 (1)
Gavia stellata	p	78.1	1621.5	1.89265	3.20992	4.8	37.8 (1)
Geococcyx californianus	a	20.1	286	2.4568	1.3031	7.0	54.9 (4)
Glareola nordmanni	p	10.7	97	1.9877	1.0310	11.1	
Glareola pratincola	p	10.1	80	1.9036	1.0048	12.6	25.2 (1)
Glaucis hirsuta	a	0.7	7	0.8451	-0.1871	9.3	8.9 (2)
Grus americana	p	188.9	7497	3.8749	2.2762	2.5	
Grus canadenis canadensis	p	161.2	3460	3.5391	2.2074	4.7	
Grus canadenis tabida	p	161.2	4450	3.6484	2.2074	3.6	108.7 (3)
Grus grus	p	202.3	5500	3.7404	2.3060	3.7	
Grus leucogeranus	p	197.2	5475	3.7384	2.2950	3.6	
Gyps fulvus	a	242.0	7436	3.8713	2.3837	3.3	127.7 (2)
Haematopus bachmani	p	46.0	555	2.7442	1.6628	8.3	51.8 (2)
Haematopus ostralegus	p	41.5	526	2.7210	1.6180	7.9	43.7 (1)
Haematopus palliatus	p	46.8	644	2.8089	1.6703	7.3	
Halcyon smyrnensis	a	11.3	91	1.9609	1.0548	12.4	
Heteroscelus incanus	p	19.0	134	2.1274	1.2788	14.2	30.8 (1)
Himantopus himantopus	p	22.8	161	2.2068	1.3578	14.2	33.1 (4)
Himantopus mexicanus	p	21.0	169	2.2271	1.3222	12.4	
Jacana spinosa	p	8.0	161	2.2068	0.9031	5.0	28.4 (4)
Jynx torquilla	a	2.7	34	1.5250	0.4314	8.1	20.1 (1)
Leipoa ocellata	sp	173.0	1785	3.2516	2.2380	9.7	
Lophortyx californicus	p	8.9	175	2.2425	0.9509	5.1	41.8 (3)
Lophotis ruficrista	p	38.5	680	2.8325	1.5857	5.7	
Meleagris gallopavo	p	66.7	4300	3.6335	1.8239	1.6	121.8 (5)
Menura novaehollandiae	a	70.9	746	2.8727	1.8506	9.5	67.0 (2)
Merops apiaster	a	6.3	57	1.7528	0.8007	11.2	
Merops orientalis	a	3.1	15	1.1703	0.4932	21.0	
Merops superciliosus	a	6.2	48	1.6839	0.7902	12.8	
Numida meleagris	p	37.4	1375	3.1383	1.5724	2.7	79.0 (1)
Oceanites oceanites	sp	9.0	34	1.5315	0.9542	26.5	15.3 (2)
Opisthocomus hoazin	p	29.7	793	1.4728	2.8993		65.2 (11)
Ortalis vetula	p	56.0	414	2.6165	1.7482	13.5	65.5 (1)
Otis tarda	p	138.1	6000	3.7782	2.1401	2.3	
Otis tetrax	p	41.4	750	2.8751	1.6165	5.5	55.7 (1)
Otus brucei	a	12.6	105	2.0212	1.0995	12.0	
Otus flammeolus	a	10.4	63	1.7993	1.0179	16.5	26.2 (8)
Otus scops	a	12.3	92	1.9638	1.0899	13.4	29.8 (1)
Pachyptila desolata	sp	30.0	200	2.3010	1.4771	15.0	24.1 (1)
Pachyptila vittata	sp	32.0	196	2.2923	1.5051	16.3	
Pandion haliaetus	a	66.0	1850	3.2672	1.8195	3.6	78.1 (11)
Parus ater	a	1.1	10	1.0086	0.0337	10.6	11.8 (1)
Parus caeruleus	a	1.2	13	1.1239	0.0831	9.1	
Parus cristatus	a	1.4	10	1.0086	0.1403	13.5	12.8 (1)
Parus cyanus	a	1.3	14	1.1367	0.1074	9.3	
Parus lugubris	a	1.7	18	1.2430	0.2227	9.5	
Parus major	a	1.7	21	1.3176	0.2215	8.0	
Parus montanus	a	1.3	10	1.0086	0.1279	13.2	12.9 (1)
Passer domesticus	a	2.8	28	1.4533	0.4502	9.9	18.4 (1)
Passer hispanolensis	a	2.9	24	1.3838	0.4589	11.9	
Passer moabiticus	a	1.8	18	1.2430	0.2492	10.1	
Passer montanus	a	2.1	23	1.3560	0.3243	9.3	17.1 (2)
Passer simplex	a	1.9	20	1.2900	0.2756	9.7	
Pedionomus torquatus	p	9.8	75	1.8751	0.9933	13.1	
Pelecanoides urinatrix	sa	20.0	124	2.0934	1.3010	16.1	24.2 (3)
Pelecanus erythrorhynchus	a	150.0	9050	3.9566	2.1761	1.7	113.7 (2)
Pelecanus occidentalis	a	112.0	3174	3.5016	2.0492	3.5	85.4 (3)
Pelecanus rufescens	a	116.0	5200	3.7160	2.0645	2.2	
Phaethon leturus	sa	45.0	392	2.5933	1.6532	11.5	30.0 (3)
Phaethon aethereus	sa	54.0	750	2.8751	1.7324	7.2	37.1 (1)
Phaethon rubricauda	sa	71.0	645	2.8096	1.8513	11.0	36.9 (2)
Phalacrocorax aristotelis	a	51.0	1598	3.2036	1.7076	3.2	57.5 (1)
Phalacrocorax atriceps	a	60.0	2948	3.4695	1.7782	2.0	58.8 (2)
Phalacrocorax auritus	a	48.0	1540	3.1875	1.6812	3.1	59.3 (5)
Phalacrocorax carbo	a	58.0	1936	3.2869	1.7634	3.0	63.3 (10)
Phalacrocorax olivaceus	a	37.0	1800	3.2553	1.5682	2.1	
Phalacrocorax pelagicus	a	40.0	1759	3.2453	1.6021	2.3	50.1 (2)
Phalacrocorax penicillatus	a	51.0	2252	3.3525	1.7076	2.3	64.8 (3)
Phalacrocorax pygmaeus	a	23.0	603	2.7800	1.3617	3.8	
Phalacrocorax urile	a	48.0	1788	3.2524	1.6812	2.7	61.8 (3)
Phalaropus fulicarius	p	8.0	131	2.1169	0.9031	6.1	19.3 (1)
Phalaropus lobatus (Alaska)	p	6.4	37	1.5705	0.8062	17.2	17.3 (13)
Phalaropus lobatus (Ontario)	p	6.2	39	1.5911	0.7924	15.9	

species	development category	egg mass (g)	female mass (g)	log female mass	log egg mass	egg / female mass %	mm (n) mean femur
Phalaropus tricolor	p	9.0	68	1.8331	0.9542	13.2	21.9 (1)
Pharomachus mocinno	a	17.0	206	2.3139	1.2304	8.3	
Phoenicopterus ruber	p	142.7	2530	3.4031	2.1544	5.6	86.6 (8)
Picoides albolarvatus	a	4.4	59	1.7723	0.6435	7.4	32.5 (2)
Picoides arctica	a	4.8	71	1.8500	0.6812	6.8	24.4 (11)
Picoides arizonae	a	3.9	44	1.6444	0.5868	8.8	
Picoides borealis	a	4.2	48	1.6767	0.6182	8.7	
Picoides dorsalis	a	5.1	67	1.8228	0.7076	7.7	22.6 (11)
Picoides nuttallii	a	2.9	38	1.5832	0.4683	7.7	
Picoides pubescens	a	2.1	29	1.4564	0.3222	7.3	16.7 (9)
Picoides scalaris	a	2.9	30	1.4814	0.4624	9.6	
Picoides villosus	a	4.4	76	1.8791	0.6435	5.8	24.3 (10)
Plegades falcinellus	p	38.5	605	2.7818	1.5858	6.4	
Pluvialis apricaria	p	35.4	214	2.3304	1.5489	16.5	35.7 (2)
Pluvialis dominica	p	27.0	154	2.1875	1.4314	17.5	33.0 (1)
Pluvialis squatarola	p	35.2	214	2.3304	1.5465	16.4	37.4 (3)
Podceps nigricollis	p	22.8	319	2.5031	1.3579	7.2	31.2 (4)
Podiceps auritus	p	21.0	392	2.5927	1.3222	5.4	32.7 (6)
Podiceps grisegena	p	38.3	1052	3.0222	1.5826	3.6	46.9 (18)
Podiceps podiceps	p	21.6	358	2.5539	1.3336	6.0	
Psophia crepitans	p	72.6	1250	3.0969	1.8612	5.8	15.7 (1)
Psophia leucoptera	p	83.2	1256	3.0990	1.9201	6.6	
Pterocles alchata	a	21.9	225	2.3522	1.3399	9.7	
Pterocles coronatus	a	15.9	300	2.4771	1.2026	5.3	
Pterocles exustus	a	12.4	192	2.2822	1.0919	6.5	
Pterocles lichtensteini	a	15.7	248	2.3945	1.1947	6.3	
Pterocles orientalis	a	21.1	383	2.5832	1.3245	5.5	47.2 (1)
Pterocles senegallus	a	17.6	255	2.4065	1.2460	6.9	
Puffinus assimilis	sp	32.0	222	2.3464	1.5051	14.4	23.7 (1)
Puffinus gravis	sp	102.0	870	2.9395	2.0086	11.7	
Puffinus ilherminieri	sp	35.0	163	2.2122	1.5441	21.5	
Puffinus navitatus	sp	63.0	324	2.5105	1.7993	19.4	
Puffinus puffinus	sp	58.0	450	2.6532	1.7634	12.9	31.0 (1)
Puffinus tenuirostris	sp	82.0	530	2.7243	1.9138	15.5	36.9 (4)
Rhea americana	p	609.3	23000	4.3617	2.7848	2.6	180.4 (11)
Rhynchotus rufescens	p	38.0	928	2.9673	1.5798	4.1	71.1 (4)
Rhynochetos jubatus	sp	67.5	900	2.9542	1.8293	7.5	
Rissa brevirostris	sp	49.4	367	2.5647	1.6937	13.5	
Rissa tridactyla	sp	55.4	388	2.5883	1.7435	14.3	37.3 (9)
Rostratula benghalensis	sp	12.0	121	2.0828	1.0777	9.9	
Rynchops niger	sp	26.9	254	2.4048	1.4298	10.6	34.8 (2)
Scopus umbretta	a	31.0	423	2.6258	1.4914	7.3	46.8 (1)
Spheniscus demersus	sp	103.0	2960	3.4713	2.0128	3.5	74.0 (2)
Spheniscus humboldti	sp	109.0	4200	3.6232	2.0374	2.6	79.0 (3)
Spheniscus magellanicus	sp	120.0	4900	3.6902	2.0792	2.4	76.3 (2)
Stercorarius longicaudus	sp	44.3	307	2.4874	1.6467	14.4	36.2 (5)
Stercorarius parasiticus	sp	51.6	499	2.6981	1.7130	10.3	38.4 (10)
Stercorarius pomarinus	sp	68.0	829	2.9186	1.8325	8.2	45.8 (1)
Stercorarius skua	sp	91.7	604	2.7810	1.9626	15.2	
Strix aluco	a	38.5	524	2.7193	1.5853	7.3	60.8 (4)
Strix nebulosa	a	52.6	1267	3.1028	1.7211	4.2	88.9 (11)
Strix occidentalis	a	49.0	663	2.8215	1.6899	7.4	67.9 (10)
Strix uralensis	a	37.3	863	2.9360	1.5717	4.3	
Strix varia	a	45.5	873	2.9408	1.6580	5.2	74.6 (15)
Struthio camelus	p	1480.0	63000	4.7993	3.1703	2.3	289.2 (15)
Sula abbotti	sa	112.0	1500	3.1761	2.0492	7.5	
Sula bassana	sa	105.0	3090	3.4900	2.0212	3.4	
Sula capensis	sa	105.0	2670	3.4265	2.0212	3.9	
Sula dactylatra	sa	78.0	1902	3.2791	1.8921	4.1	61.2 (2)
Sula leucogaster	sa	54.0	1382	3.1405	1.7324	3.9	
Sula nebouxii	sa	61.0	1840	3.2648	1.7853	3.3	
Sula serrator	sa	94.0	2350	3.3711	1.9731	4.0	
Sula sula	a	58.0	1030	3.0128	1.7634	5.6	47.0 (2)
Sula variegata	sa	76.0	1410	3.1492	1.8808	5.4	54.9 (1)
Trogon elegans	a	8.2	74	1.8681	0.9164	11.2	
Turnix sylvatica	p	3.4	40	1.5966	0.5361	8.7	
Tyto alba	a	26.6	57	1.7551	1.4249	46.7	58.1 (26)
Upupa epops	a	4.5	61	1.7882	0.6532	7.3	22.4 (1)
Uria aalge	s	109.0	1001	3.0004	2.0374	10.9	48.6 (6)
Uria lomvia	sp	106.0	932	2.9694	2.0253	11.4	47.5 (5)
Zenaida asiatica	a	7.7	153	2.1847	0.8865	5.0	
Zenaida macroura	a	6.5	116	2.0626	0.8129	5.6	27.3 (4)
Confuciusornis sanctus	p	8.2					47.0 (15)

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